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VI. Croonian Lecture.—*On the Mammalian Nervous System, its Functions, and their Localisation determined by an Electrical Method.*

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(*From the Physiological Laboratory of the University of Oxford.*)

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[Plates 29–35.]

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CHAPTER I.—INTRODUCTION, INCLUDING THE AUTHORS' METHOD AND THE PLAN OF THE RESEARCH.

In the 'Proceedings of the Royal Society,' vol. 45, 1889, p. 18 (Meeting of November 1, 1888), we published a preliminary account of some of the experiments of which the results are now given in full detail.

In that communication we stated that the object of our work then was to endeavour to ascertain the character of the excitatory processes occurring in nerve fibres, when, either directly (artificially) excited, or when in that state of functional activity, which is due to the passage of impulses along them from the central apparatus. The most important way in which such a method could be applied was obviously one which would involve the investigation of the excitatory changes occurring in the fibres of the spinal cord when the cortex cerebri is stimulated. We must at once assume that the motor side of the central nervous system is practically divisible into three elements:— 1. Cortical centres. 2. Efferent (pyramidal tract) fibres leading down through the internal capsule, corona radiata, and spinal cord. 3. Bulbo-spinal centres contained in the medulla and the spinal cord, and forming the well-known nuclei of the cranial and also of the spinal motor nerves.

It had already been determined, both by direct observation and by the graphic method (1) that certain areas of the cortex were connected with definite movements of various parts of the body, and (2) that while the complete discharge of the cortical apparatus was followed by a very definite and characteristic series of contractions of the muscles in special relation with the particular point excited, the effectual removal of the cortical central mechanism and subsequent excitation of the white fibres passing down through the internal capsule, &c., led to the production of only a portion of the effect previously obtained from the uninjured brain.

This method of observation in no wise showed what processes were actually occurring in the spinal and other nerve fibres, and although the ablation of the cortical centre, to a certain degree suggested the extent to which the cortex acted, nevertheless, it did not afford an exact demonstration of the same. Moreover, the data which the graphic method furnished were precluded, through their being muscular records, from determining what share, if any, the lower bulbo-spinal central nerve cells took, either in the production of the characteristic sequence of contractions or in the modification, whether in quality or in force of the descending nerve impulses during their transit.

It seemed to us that the only way to approach this subject would be to get, as it were, between the cortex and the bulbo-spinal system of centres. This would be accomplished if some means were devised of ascertaining the character of the excitatory processes occurring in the spinal fibres of the pyramidal tract, when upon excitation of the cortex, nervous impulses were discharged from the cortical cells and travelled down the cord.

The question as to the extent to which it is possible to obtain physical evidence of the actual presence in nerve fibres of excitatory processes and thus to arrive at reliable data for the comparison of their amounts is one which, up to the present, has been answered only indirectly, and that in two ways, firstly, by the extension of Helmholtz's classical experiment of determining the rate of transmission, and secondly, by observing those variations of electrical states in nerve fibres which

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DU BOIS-REYMOND discovered to be invariable concomitants of excitatory processes. As will subsequently be shown in the historical retrospect, it is well known, through the researches of DU BOIS-REYMOND and others, that the fibres of the spinal cord, just as nerve fibres in the peripheral trunks, are characterised by showing when unexcited an electrical difference between their longitudinal surface and cross-sections, and furthermore, that when excited a well-marked diminution of this resting electrical state is produced in the fibres of the cord as in those of nerve trunks.

Now since such excitatory variations in the electrical state are presumably parallel in time and amount with the presence in the nerve of the unknown processes termed excitatory, which a series of stimuli evokes, it was reasonable to presume, if the cortex were discharging a series of nerve-impulses at a certain rate down the pyramidal tract, that there would be a series of parallel changes in the electrical condition of the fibres in the cord tract, and that with a suitable apparatus for responding to such changes these might be both ascertained and recorded.

If this could be done, then the character of the discharge of the cortical centre into the spinal cord would be, for the first time, definitely ascertained.

As has been said before, the graphic method to some extent suggested the solution of the problem, but the graphic method could not exclude, as this newer mode of investigation does, the bulbo-spinal centres. Judging from the rate of contractions of the muscles convulsed by excitation of the cortex, it was reasonable to expect that the variations in the electrical condition of the pyramidal tract might intermit fifteen or twenty times per second. If, therefore, they were to be observed or recorded, it was obvious that some instrument would have to be used capable of quickly responding to very minute electrical differences succeeding one another at very short intervals of time. The only instrument available for this task is LIPPMANN'S electrometer, and, as we have stated in our previous communication, we had the advantage of the assistance of Mr. G. F. BURCH in obtaining several very sensitive instruments.

This instrument in addition presents the invaluable advantage of its movements being easily recorded by photography, as originally described by BURDON SANDERSON and PAGE. Such records are given in our previous paper in the 'Proceedings'; they were from the first so definite, and so constant, that they enabled us at once to pass on to a further development of the same method. It occurred to us that the method afforded a means, not only of discovering the rhythm of the nerve disturbances as they pass along the spinal channels, but also of investigating the line of communication existing between separated nerve centres, the mode of discharge of such centres, and the determination of the direct paths, whether afferent or efferent in the structure of the central nervous system. It is this last wider application of the method to which we wish particularly to draw attention in the following pages, inasmuch as although it has hitherto been possible by means of division or ablation of certain portions of the central nervous system, *e.g.*, the spinal cord, to trace by

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the loss of function the probable paths of transmission of afferent or efferent impulses, yet such a mode of experimentation is always open to very grave disadvantages and sources of fallacy. Such, for example, is the always recurring possibility of functional changes proceeding beyond the desired lesion, &c.

The accomplishment of this further purpose, viz., the localisation of both paths and centres by ascertaining the excitatory electrical effects in relation with them, was one of the main objects we had in view.

In carrying it out we found it was unnecessary to employ the electrometer, and, in fact, that it was advantageous to use the galvanometer, the record of which could be more easily and more accurately noted, since its graduation admits of far higher magnification. Moreover, with this instrument it was possible, by employing a series of stimuli, of known number and duration, to obtain quantitative results of definite comparative value, as will be shown further on; and thus to compare the electrical effects evoked (1) in different central paths by direct stimulation of these, and (2) in any one path by excitation of different regions.

The plan upon which the present paper is framed is, first, to give a historical retrospect of the work of authors who have opened up the study of electrical changes in the central and peripheral nervous system; second, to describe at length our mode of experimentation, with special reference to the modifications which we have introduced, then to compare roughly the results we have obtained by our present method with those which had been previously ascertained by the graphic method, and so introduce the description of the facts which we have discovered, elucidating the physiology of the spinal cord both in its relation to the higher centres and to the peripheral nerves. In describing the detailed results of our experiments we have found that it is difficult, from the extent of ground covered by the subject, to adopt a convenient arrangement of facts, and mode of describing the same, which are free from the fault of repetition. We finally determined to gather the results together into definite groups, each associated with the excitation and investigation of particular regions, and refer in the briefest manner to any important principles which were not directly elucidated by, but only involved in, the particular experiments under consideration. Finally, we give at length a summary of the general conclusions which we consider we are justified in drawing from our experimental results.*

* We here wish to express our great indebtedness to Professor Burdon Sanderson for placing at our disposal the instruments and equipment of the Physiological Laboratory of the University of Oxford. We are also under especial obligations to Mr. G. F. Burch, whose constructive skill provided us with the requisite electrometers, and who very kindly gave his assistance in preparing our photographic records.

Finally Dr. Howard Tooth has very obligingly carried out the laborious task of the microscopical investigation of the spinal cords in those cases where we performed the section of columns antecedently to the special experiments of the present research.

The expenses of the present investigation have been defrayed by grants from the Scientific Grants Committee of the Royal Society, and from the Scientific Grants Committee of the British Medical Association.

CHAPTER II.—HISTORICAL.

We consider it advisable to give a brief sketch or rather catalogue of the chief facts which have been ascertained concerning the specific function of nerve centres, and the conductivity of nerve fibres, so far as the central nervous system is concerned, in order that the various points we raise in the rest of the paper may be rendered more intelligible when the results obtained by our method are contrasted with those discovered by other means. It is naturally impossible for us to give on the present occasion a complete history of this vast subject; we would only, therefore, allude to those points towards the further elucidation of which we have directed the present research. The procedures employed by various authors with the exception of the galvanometric method may be enumerated as follows :—

1. Electrical and other stimulation with direct observation of the phenomena evoked.

2. Stimulation with graphic record of muscular and other movements produced.

3. The method of anatomically observing the degeneration of nerve fibres consequent upon their separation from nerve centres with which they are in functional relation.

4. The embryological method of observing the development or differentiation of tracts and fibres.

Of the foregoing methods, the first was the one by means of which the principles of localisation were earliest determined, and in this connection it is scarcely necessary to do more than allude by name to Hitzig and Fritsch, Ferrier, Munk, Luciani, Albertoni, and others. The results they obtained are to be classed with those gained by means of the second method of recording muscular and other movements, employed in the analysis of the functions of the central nervous system for the first time by François Franck and Pitres, and in the subsequent investigations of Bubnoff and Heidenhain. They are open to the same objection, viz., that since they involve motor function they necessarily exhibit the activity of two sets of central mechanisms, and that therefore they only indicate the functions of the paths which run in the central nervous system in so far as these functions are modified by those paths being intimately connected with the lower or bulbo-spinal centres.

The degeneration method, in which localisation of a nerve path is accomplished by means of studying the retrograde changes which nerve fibres undergo when they are cut off from the lowest nerve centre, with which they are in relation, should they happen to be paths for ascending transmission, or *vice versâ* from the highest nerve centre for descending transmission was initiated by Türck and followed up more especially by Charcot and his pupils, as well as by a large number of investigators, and neuro-pathologists of all countries. This method is not free from possible error, since in the case of nerve channels connected at each end with central structures, we do not yet know what the nature of the connection must be which enables the nerve channel to successfully resist degeneration. Therefore, while the

existence of degeneration furnishes us with positive evidence as to the presence of a direct path, its absence does not exclude the existence of such a path.

The embryological method, which affords a very fair control of the degeneration method, was instituted by FLECHSIG and has since been extended by BECHTEREW and others. It gives a fair indication of the proportionate number or quantitative relation of the elements which go to make up any one channel, whether direct or indirect, but beyond this, and the all important localisation of position, it does not carry us. By a special histological method, introduced by GOLGI, the anatomical relation of the paths in the developing cord have recently received a fuller demonstration, at his hands as well as KÖLLIKER'S, RAMÓN Y CAJAL'S and others.

It will be convenient to tabulate the facts according as they relate to

I. Centres.

II. Paths.

I. CENTRES.

Functional Activity of Centres.

As regards Centres, the position assumed in the introduction* is, we believe, as a matter of fact, tacitly in the minds of observers, if not admitted, and the influence of "basal centres" is not so overwhelmingly important as originally supposed by the older observers. To conveniently combine, therefore, the results without doing violence to the theoretical views expressed by anyone, it is only necessary to arrange the facts in relation to the part which is the seat of experimental investigation.

A. *Cortex.*

(1.) *Latent Period.*—The loss of time which intervenes between the application of the stimulus to the cortex and the commencement of the resulting muscular contraction is ·06 on the average in the Carnivora. (FRANCK and PITRES, BUBNOFF and HEIDENHAIN, SCHÄFER, ourselves.)

(2.) *Excitability.*—This property of the cortex is greatly altered, *i.e.*, either increased, or diminished by—

(*a*) Severe hæmorrhage ; (*b*) deep anæsthesia ; (*c*) cooling ; (*d*) drying ; (*e*) fatigue ; (*f*) peripheral stimulation of the functionally corresponding and other parts of the body. (BUBNOFF and HEIDENHAIN, BUZZARD, EXNER.)

The latent period may vary from the effect of any of these causes as well as from the intensity of the stimulus. (BUBNOFF and HEIDENHAIN and other authors.)

* Viz., that the plan of the central nervous system, as regards its "motor" side, consists in a cortical mass of grey matter, and a corresponding mass in the bulbo-spinal part of the central neural axis, with segmental representation of function, while that finally these two great central apparatuses are connected by the direct paths known as the pyramidal tract or excitable fibres of the corona radiata internal capsule, and, we must add, of the lateral column of the spinal cord. According to this view the basal centres and cerebellum act on the direct motor apparatus, if at all, as reinforcing mechanisms.

(3.) *Mode of Discharge.*—The impulses generated in the cortex, and which pass down to the muscles may, according to the duration and intensity of the stimulus, be of the nature of (*a*) single discharges producing one muscular contraction; or (*b*) compound discharges producing tonic muscular contraction, or (*c*) a combination of tonic and clonic contractions. (Fritsch, Hitzig, Ferrier, Munk, Franck, and all other authors.) This last combination is to be looked upon as the complete discharge of the cortex, *vide infra* and pp. 345, 349, &c.

(4.) *Nature of the Discharge.*—(*a.*) The single muscular contraction is more prolonged, and ceases more gradually than that elicited by a single stimulus applied to the motor nerve. (Franck, confirmed by ourselves.)

(*b.*) The tonic contraction is regarded by most authors as a fusion of contractions evoked by many discharges. (Franck, Schäfer and Horsley; *vide infra* "*Corona Radiata.*")

(*c.*) The tonic and clonic contractions occur in the order mentioned, and are to be regarded as the muscular response to a complete cortical discharge, *i.e.*, comprising a primary effect and after-effect.

(*d.*) The rate or rhythm with which these muscular responses* appear to succeed one another has been variously estimated by different observers in different animals and with different instruments, and has been ascertained to be from 8 to 10 per second.

(5.) *Relation of the Discharge to the Parts of the Body.*—(*a.*) Localisation of the representation of the gross divisions of the body to definite areas of cortex. (Fritsch and Hitzig, Ferrier, Munk, Luciani, Schäfer, Beevor, Horsley.)

(*b.*) Localisation of the representation of segments of the gross divisions to definite areas of cortex. (Beevor and Horsley.)

(*c.*) Localisation of the representation of the character of the various movements of segments to definite areas of cortex. (Beevor and Horsley.)

B. *Spinal Cord.*

Under this heading we will group the phenomena associated with the functional activity of the system of bulbo-spinal centres, *i.e.*, those in which the efferent paths terminate. It may not be superfluous to add that the information furnished by the graphic method does not differentiate the complex structure of a bulbo-spinal centre, and that it can only yield a record of the combined action of mainly afferent and mainly efferent corpuscles in the posterior and anterior divisions of the grey matter. All methods of observation hitherto employed involve the activity of the whole apparatus, and this must be borne in mind in considering the following facts.

* The tracing waves indicating the contractions are frequently summated. (Horsley.)

Quite recently the value of these waves as indications of rhythmical nerve discharges has been contested. (Wedenskii, Haycraft.)

(1.) *Latent Period.*—The interval of time occupied in the passage of a nerve impulse from the afferent to the efferent side of a (reflex) bulbo-spinal centre is given on p. 481, to which reference is directed. (WUNDT, EXNER, and others.)

(2.) *Excitability.*—This function of the grey bulbo-spinal matter is modified by the same causes as those which influence the Cortex, see pp. 272 and 483.

When the excitability of the cord is raised, *e.g.*, that of the distal segments after section, these latter may discharge in a coordinated fashion, see p. 423, as was first observed by SCHIFF.

(3.) *Mode of Discharge.*—The bulbo-spinal centres, like the cortex, present three modes of discharge, but not in the same degree, *e.g.*, the combined sequence of tonus and clonus though sometimes present, see pp. 483–499, nevertheless occurs but rarely. Further, as evidenced by muscular responses, the bulbo-spinal centres appear to discharge at regular intervals under certain conditions of isolation and excitation, *e.g.*, ankle clonus (V.H.). For further detail see p. 483.

(4.) *Nature of the Discharge.* (*a.*) As in the case of the cortex cerebri the character of the muscular response to excitation of the cord is different from that seen when the excitation is directly applied to the nerve.

(*b.*) The tonic contraction is usually developed more rapidly than that obtained from the corona radiata.

(*c.*) The rhythm of the intermittent muscular contractions, fused or not, is from 8 to 10 per second or frequently the early multiples of this rate.

(5.) *Relation of the Discharge to the Parts of the Body.*—(*a.*) Localisation of the representation of the gross divisions of the body to different regions of the bulbo-spinal apparatus is well marked. (All authors.)

(*b.*) Localisation of the representation of the segments of the gross divisions and the character of their respective movements to different root-origins in the grey matter. (FERRIER and YEO, SCHIFF, FORGUE, BEEVOR.)

II. PATHS.

Functional Activity of the Efferent Paths.

The graphic method only permits of a limited analysis of paths, *i.e.*, fibres, inasmuch as there is of necessity included the bulbo-spinal system of centres for the purpose of giving the muscular contractions used for record. Hence no result by the graphic method can be regarded as pure; moreover, it only furnishes information upon the functions of efferent paths.

In fact, there is no direct evidence forthcoming from any method of observation, except that of the galvanometer, to prove that the paths themselves in the cord are excitable. Indeed, it has long been held by many physiologists that all effects obtained from stimulation of the spinal cord are due to primary and progressive

excitation of reflex centres (SCHIFF, CHAUVEAU). Consequently, it must be understood that the following enumeration of facts is written and arranged in the light of our experimental results, set forth in the present paper.

A. *Corona Radiata.*

(1.) *Latent Period.*—The loss of time intervening between the moment of application of the stimulus to the corona radiata and the commencement of the resulting muscular contraction is usually ·04 sec. (FRANCK and others.)

(2.) *Excitability.*—The excitability of the fibres rapidly fails upon their exposure. VULPIAN showed that relatively the excitability of the corona radiata was higher than that of the cortex. In this he was confirmed by the observations of BOCHEFONTAINE, COUTY, ASCH and NEISSER, and others.

(3.) *Mode of Discharge.*—The muscular contraction may be (*a*) a single twitch, or (*b*) a tonus. The combination we have termed the complete cortical discharge, and consisting of tonus and clonus, is never seen where the cortex is absolutely removed. (FRANCK, BUBNOFF and HEIDENHAIN in part, HORSLEY, SCHÄFER and HORSLEY.)

(4.) *Nature of the Discharge.*—(*a.*) The tonus observed is regarded as a fusion of muscular responses which commence and end sharply with the beginning and end of the excitation.

(*b.*) The rate of recurrence of the individual responses is unknown.

(5.) *Relation of the Discharge to the Parts of the Body.*—Localisation of gross divisions of the body to certain fields of fibres issuing from cortical centres (all authors named above).

B. *Internal Capsule.*

(1.) *Excitability.*—The excitability of the fibres forming the internal capsule is very high. (FRANCK, GLIKY, BEEVOR and HORSLEY.)

(2.) *Mode of Discharge.*—Indistinguishable from that of the corona radiata, *quod vide.*

(3.) *Nature of Discharge.*—Ditto.

(4.) *Relation of the Discharge to the Parts of the Body.*—(*a.*) Localisation of the representation of the gross divisions of the body to limited fields of fibres. (FRANCK and PITRES, GLIKY, BEEVOR and HORSLEY.)

(*b.*) Localisation of the representation of segments of the gross divisions of the body to definite fields of fibres. (BEEVOR and HORSLEY.)

(*c.*) Localisation of the representation of the character of various movements of segments to definite fields or bundles of fibres. (BEEVOR and HORSLEY.)

C. *Crus Cerebri.*

(1.) *Excitability.*—The excitability of the fibres has been determined by many observers. (BUDGE and others.)

(2.) *Relation of the Discharge to Parts of the Body.*—Localisation of the representation of the gross divisions of the body to certain fields of fibres. (BRISSAUD and others.)

D. *Spinal Cord.*

It will be scarcely realised, except by those who have made a special study of the literature of the physiology of the spinal cord, how little has been done which would enable us to carry out, strictly speaking, the differentiation of the subject of conduction in that organ, by arranging the facts in the same way as we have just done for the higher parts of the nervous system. So much so is this the case that we do not intend to do more at this stage than indicate what we believe to be a fair estimate of the experimental work already accomplished. In introducing our own work later on, which directly bears on the points at issue, we shall draw attention to many of the more salient details which require attentive discussion. We will, therefore now content ourselves with furnishing a general review of the function of conduction in the cord. We may note in passing that almost all the literature is to be found in the writings of VON BEZOLD, ECKHARD, GRÜNHAGEN, SCHIFF, IMMANUEL MUNK, and others. We would, in the first place, urge, what we have reason to do with greater weight later, that not one of the foregoing methods, *i.e.*, graphic degeneration, embryological, &c., is capable of answering the question of conduction or its localisation in an absolute manner. The great difficulty in considering conduction by the cord is the disseverance of the action of the bulbo-spinal centres from that of the nerve fibres which happen to pass through or by them, and this difficulty does not appear to us to have met with the amount of attention that it would naturally seem to deserve. In fact, to our mind the galvanometric method is the only means within our reach at present by which a solution can be arrived at, and even that method requires to be considerably further elaborated.

Dividing conduction in the spinal cord into the two great classes of—

1. Conduction of impulses downwards;
2. Conduction of impulses upwards;

we are able to summarise the facts which appear to be thoroughly reliable as follows :—

(1.) *Conduction of Impulses downwards.*—In Man and the highest Apes direct conduction downwards, *i.e.*, from the cortical centres to the bulbo-spinal system, appears to be provided for in the upper half of the spinal cord by both the anterior column, close to the margin of the anterior fissure, and, speaking roughly, by a triangular area in the posterior part of the lateral column, just external to the posterior horn of grey matter.

(2.) *Conduction of Impulses upwards.*—There is known to be an entrance from each posterior root into the postero-external column of fibres, which run directly from the ganglion of the posterior root as high as the medulla oblongata. These direct fibres

are further known to gradually tend towards the middle line of the cord as they are displaced by others entering the cord in proceeding upwards. Further these direct fibres are strictly unilateral, so far as is known at the present time.

There are, in addition, also other known systems of ascending channels, but these are not directly continuous with the root, but start indirectly from central mechanisms which, to judge from the degeneration method, although this is of course not absolute, appear to intervene. These are (1) the direct cerebellar tract which runs up the posterior and outer surface of the lateral column, and (2) the antero-lateral tract which occupies a similarly lateral position further forwards on the margin of the cord.

In addition to the foregoing, there is some evidence to show that internuncial fibres run in the lateral column in about the inner third of its centre, or a little posteriorly to this point. Of the existence of channels for transmission of impulses upwards in the opposite posterior column to the side of the root by which they enter the cord nothing is known for certain.

History of the Galvanometric Method of Determining the Action of the Nerve Centres and the Course of Nerve Channels.

As we have before frequently acknowledged, the real basis of the galvanometric method was the discovery by DU BOIS-REYMOND* of the negative variation produced by excitation in the resting electrical difference of a nerve path. Since that discovery, the idea has doubtless occurred to various physiologists that, by this means, we might discover the mode of functional activity of nerve centres. CATON† was the first to our knowledge who directly employed the galvanometric method of determining such variations for the investigation of the activity of nerve centres, and the localisation of the same. He connected points on the external surface of the cortex with the galvanometer, and he found that the uninjured external surface of the brain was usually positive to a section of the same. When any part of the cortex thus investigated was thrown into activity, the resting difference showed distinct negative variations. Thus, in the Monkey, after the cortex had been prepared and the electrodes applied to the centres (FERRIER) of rotation of the head and mastication, the negative variation or action current showed itself when these movements were performed. Further, in the Rabbit, when the area of the cortex which subserves the movements of the eyelids was investigated, the negative variations showed themselves when the opposite retina was illuminated. SETSCHENOW‡ was the first to our knowledge who connected the medulla oblongata with the galvanometer. He noticed certain periodic variations in the resting electrical difference, which he attributed to periodic changes of the functional activity in the bulbar centres.

* 'Untersuchungen über Thierische Elektricität.'

† 'British Medical Journal,' 1875; also 'Transactions of the IX. International Medical Congress, 1887.'

‡ 'Archiv für gesam. Physiologie,' PFLÜGER. vol. 25, 1881, p. 281.

We commenced our researches in 1888, and published a preliminary account of the same as stated in the introduction to the present paper. Moreover, we demonstrated our method in 1889 before the Physiological Society, and further, at the International Physiological Congress, held in Basle, in September, 1889, we made a general communication on the method, and showed a complete experiment to the physiologists there assembled. An abstract of our paper in the 'Proceedings of the Royal Society,' was published in the 'Centralblatt für Physiologie,' 1889, and the account of the demonstration at Basle was published in October, 1889, not only in the 'Centralblatt für Physiologie,' but in the 'Progrès Médical,' 1889, and elsewhere. We have published, on the occasion of a priority discussion presently to be alluded to, in the 'Centralblatt für Physiologie,' 1891, the various publications we have made of our method arranged in chronological order. It was not until the close of 1890 that we learned that the galvanometric method was being employed abroad. On the 8th November, 1890, there appeared in the 'Centralblatt für Physiologie,' a paper by Dr. A. Beck, of Cracow, who, ignorant apparently of our publications and demonstrations, described the galvanometric method, and pointed out the value of it in determining the localisation of contripetal or afferent nerve function in the brain and spinal cord. This paper, however, was really but an abstract of a full paper which was presented to the Academy of Science in Cracow, in 1890, a copy of which we owe to the kind courtesy of Professor Cybulski, and in which is given a brief reference to the Basle demonstration, but no reference to our publications in 1888, or to Professor Biedermann's abstract of the same in the 'Centralblatt für Physiologie,' 1889. The appearance of this paper produced a priority reclamation by Professor Ernst Fleischl von Marxow, of Vienna, published in the 'Centralblatt für Physiologie,' on the 6th of December, 1890. In this communication Fleischl showed that, as long ago as the 7th of November, 1883, he had deposited in the archives of the Imperial Academy of Science in Vienna a sealed letter, in which he announced that he had employed the galvanometric method for the same purpose, *vide infra*, as Beck and with the same details. Fleischl, in this reclamation, does not mention any more than Beck, the prior investigations of Caton, or our publications and demonstrations of the last three years. Although Fleischl appears to have independently thought of employing the galvanometer as an index of functional activity in the nerve centre, when it is the seat of centripetal or afferent disturbance, his method of recording his idea in a sealed note, discounts the credit that otherwise might fall to him. All these authors have dealt with the employment of the galvanometer as an index of the changes going on in the nerve centre, *i.e.*, nerve corpuscles, when that nerve centre is directly connected with the instrument. We will allude directly to the results obtained by Beck and by Fleischl, but we wish to point out that from our own observations made in the same way, we are not at present satisfied that the basis of these researches is entirely trustworthy (see Chapter IX.), and that they deal with but one point in this extensive subject. So far as we are aware, we were the first to determine by use of the electrical

method the localisation and quantitative estimation of either centripetal or efferent impulses issuing from nerve centres in functional activity, and, in addition, we first employed it for the determination of the localisation of paths or channels of nerve function, particularly in the spinal cord. After this preliminary statement, which has been rendered necessary by the publications referred to, we will refer to the results which were obtained by FLEISCHL and BECK respectively, although, as we said just now, these results are, we consider, for the reasons we discuss on p. 296, not to be immediately accepted. FLEISCHL (*loc. cit.*) connected, by means of non-polarisable electrodes, two symmetrical points on the surfaces of the cerebral hemispheres with the galvanometer, and found that in the resting condition there was little or no electrical difference. If, however, a sensory end organ, whose corresponding area of the cortex was thus connected, were excited, the effect produced was an electrical difference as recorded by the deflection of the galvanometer. This effect he especially obtained when the visual centre discovered by MUNK was connected with the galvanometer and the eye illuminated, whereas little or no difference followed excitation of cutaneous nerve endings. Finally, he found that profound narcosis with chloroform or ether abolished this effect, and that special precautions must be taken against cooling of the preparations.

BECK (*loc. cit.*) removed the brain, spinal cord, and sciatic nerve of the frog *en bloc* and placed the preparation on a glass plate; he then applied non-polarisable electrodes made of kaolin and 0·6 per cent. salt solution to the longitudinal surface of the spinal cord and connected them with a Hermann's galvanometer. He found that there was constantly an electrical difference of such a nature that the centripetal, *i.e.*, proximal parts of the nervous system were always electro-negative to centrifugal or distal parts. If then the sciatic nerve were excited this primary difference was increased, provided the galvanometer electrodes were placed above the lumbar enlargement. If, on the other hand, the sciatic nerve were excited while one of the non-polarisable or leading-off electrodes were placed on the lumbar enlargement, there was observed a negative variation of the primary difference. In another series of experiments on Dogs and Rabbits he connected two points of the surface on one hemisphere with the galvanometer, and found that there were more or less regular swaying movements of the needle, and which he regarded as "action currents." Excitation of the retina caused the visual centre of MUNK to become negative to the rest of the hemisphere.

DANILEWSKY* has quite recently published the results of five experiments which he performed in 1876, and in which he found that when non-polarisable electrodes were connected with the cerebral hemispheres (whether superficially or deeply) and with a sensitive du Bois-Reymond galvanometer negative variations of the resting difference were observable as consequences of various modes of sensory stimulation. The portion of the hemisphere from which these effects were obtained was the

* 'Centralblatt für Physiologie,' April, 1891, p. 1.

posterior part alone, and in most cases opposite to the side to which the excitation was applied.

CHAPTER III.—DETAILED DESCRIPTION OF THE METHODS EMPLOYED IN THE PRESENT RESEARCH.

The description of the methods may be best effected by considering, in succession :—

1. The method of anæsthesia employed.
2. The operative procedure.
3. The recording and exciting apparatus.
4. The general procedure and the precautions used.

Section I.—Method of Anæsthesia.

The anæsthetic employed in these experiments was, in almost all cases, ether, the exceptional cases being those in which some bronchial or nasal catarrh rendered it advisable to substitute chloroform, this latter giving a more even and steady narcosis, though at greater risk to the animal.

The physiological action of ether has received considerable attention lately, and a few points in connection with it are of sufficient importance as bearing upon our experiments to warrant a more detailed notice.

In the first place, it has been shown (Hooper, Semon and Horsley, Bowditch, and others) that ether when present in the circulating blood through inhalation, appears to have a distinctly differential effect upon the two kinds (red and white) of muscle, or upon their innervation, *i.e.*, centres, fibres, or nerve endings.

Further that the direct application of the liquid or vapour of ether to the trunk of a nerve causes paralysis of its physiological conductivity.* (Hooper and Biedermann.)

The investigations of Flourens† in 1847 had elicited the fact that the inhalation of ether produced physiological effects, in which the functional activity of the reflex centres was abolished before that of the conducting nerve paths, and this has been substantiated by the work of other investigators.

It is with special reference to the action of ether upon these two structures that the present remarks are introduced, since, with the exception of the few experiments in which we employed the graphic method, our work has been entirely confined to the study of the changes in nerve centres and nerve fibres.

It was consequently of primary importance for us to know to what extent the inhalation of ether has a differential action upon nerve centres as distinct from nerve fibres.

In this connection experiments (Horsley and Spencer) have shown that the

* Biedermann, 'Wien, Akad. Sitzber.,' vol. 97, 3 Abth., 1888.

† Flourens, 'Comptes Rendus,' vol. 24, 1847, p. 161.

instant effect of ether inhalation is a remarkable fall in blood-pressure, such a fall in blood-pressure as the early experiments of VULPIAN showed would of itself, if sufficiently pronounced, cause a diminution in the functional activity of all the nerve elements, such diminution occurring first and most markedly in the centres, and even a comparatively slight fall may be followed by a loss in the excitability of these, although the nerve fibres might not be appreciably affected.

The effect of ether, therefore, in diminishing the excitability of the cortex and lowering its functional activity may be in part due to changes in the circulation. It is probable, however, that the ether in the blood exercises a direct toxic effect upon the nerve structures, of a similar kind to that which is brought about by the direct action of the vapour already alluded to. We are not aware of any experiments as to the direct toxic action of ether vapour upon nerve centres; but it is extremely probable that such action occurs and that the centres should be affected by an amount of ether in the circulating blood which is too small to affect in any sensible degree the fibres.

Whatever the share which the two factors, blood-pressure changes and ether in the blood, may respectively have in the production of the effect, the result is that profound general narcosis serves to abolish the functional activity of nerve centres before that of nerve fibres. We have therefore made use of etherisation, with due caution, to assist us in analysing the compound excitatory effects observed when a complex structural arrangement of centres and fibres has been stimulated, and we have in all cases observed great care in noting as accurately as we could the degree, whether profound or slight, of narcosis at the time of each experimental observation.

There is one possible disadvantage in the use of large quantities of ether during a considerable period of time which is not very obvious at first sight, and that is the amount of vapour which is present in the air of the room. It did not occur to us that this could act injuriously upon the preparations under investigation until we noticed in three prolonged experiments in which, owing to the method of inhalation, a large quantity of ether was used in a warm close room, that both the exposed cortex and the sciatic nerve suddenly lost their excitability, which they did not regain. The possibility of this being due to that injurious action of the ether vapour dissolving in the liquids upon these structures, which was pointed out by BIEDERMANN, then occurred to us. The effect of the vapour in the room was increased, perhaps, by its dissolving in a warm bath containing 0·6 per cent. saline, which mixed with the blood of the animal was employed for irrigation, &c., of the nerve structures. Although the failure might have been due to other causes (exposure, &c.), still the fact of its not occurring when special precautions were taken to avoid the excessive evaporation of ether into the room and the contamination of the saline, leads us to conclude that the cause mentioned is at any rate a depressing factor which ought, as far as possible, to be excluded.

The use of chloral or morphia would undoubtedly entirely exclude any error of this

kind, but it has the enormous disadvantage that it is impossible to alter the degree of narcosis, and, as will be seen, such alteration is an essential condition in experiments of the kind which we have undertaken.

As regards the practical administration of the anæsthetic, the best results were obtained by pushing the etherisation at first to a profound degree, so as to abolish entirely superficial reflexes, and always by causing profound narcosis before performing any operation, such as division of the spinal cord, &c., which would, if the narcosis were less deep, entail depressant effects upon the centres concerned with systemic life through the damaging influence of shock. Subsequently when, the operative procedure having terminated, the actual observations were being made, the narcosis was rendered less and less intense as the slow collapse inseparable from the experimentation asserted itself. This slow collapse, since it involves the gradual failure in excitability of the nerve structures and primarily of the nerve centres, has the same effect as an anæsthetic in producing narcosis, which was preferably intensified by the administration of ether in small repeated doses rather than in few large ones.

Section II.—Operative Procedure.

1. *Exposure of the Cortex and of the Corona Radiata.*

(*A.*) *Cortex.*—The animal, having been deeply anæsthetised in the manner stated, was further immobilised on a firm support, upon which a metal vessel was placed so as to be underneath the thorax. This was kept filled with hot water and, combined with suitable coverings for preventing loss by radiation, served to keep up the temperature.

The dura mater was then exposed *lege artis* to the necessary extent and over the required region, all hæmorrhage from the bone being instantly arrested by the use of soft modelling wax, &c. As soon as the dura mater was cleared the wound was closed, and kept covered with sponges soaked in hot 0·6 per cent. saline solution, whilst the further operations necessary for the experiment were undertaken.

The cortex was finally exposed by taking up the dura mater by means of iridectomy forceps or fine curved needles, and dividing it, care being taken to keep it always protected with hot saline sponges unless an actual experiment was in progress.

(*B.*) *Corona Radiata.*—The cortex having been thoroughly exposed, a sharp scalpel was passed horizontally through the hemisphere in the plane of the centre of the coronal gyrus, and the upper and anterior thirds raised as a lid of a box. Pieces of amadou were then gently laid and pressed on the edges of the cut, thus arresting the free bleeding from the vessels of the pia mater. Care was always taken to determine precisely the topography of the section, and to accurately apply the electrodes to the fibres coming from the requisite area of the cortex. The necessity

of this care is obvious to those who are familiar with the limitation of the fibres in the corona radiata, but we think it well to mention the fact, as a malposition of 2 mm. is sufficient, with the stimulus we employed, to prevent the production of the effect.

2. *Exposure of Peripheral Nerves.*

The great sciatic nerve was usually selected for this purpose, and was exposed in the thigh for 6 centims. of its length. It was then divided near the knee, and its central end ligatured, care being taken to prevent any pull upon the structure, or any injury to the *arteria comes nervi ischiadici* which was always included in the ligature. When not required for purposes of immediate experiment it was irrigated with 0·6 per cent. saline solution, and covered over by the skin and muscular flaps. During use, whether for purposes of excitation or in connection with the non-polarisable electrodes, it was always so fixed that no movement of the animal could pull upon the structure.

3. *Preparation of the Spinal Cord for Observation.*

The spinal cord afforded naturally more difficulty in its preparation, and this requires therefore a more detailed description.

The objects in view were—

(*a.*) To expose and divide the cord.

(*b.*) To preserve as far as possible its circulation.

(*c.*) To fix the spinal column so that no accidental movements of the animal should affect it.

(*d.*) To avoid the depression due to cooling, drying, &c.

(*e.*) To secure for the purposes of electrical investigation as complete an isolation as possible of its different parts.

These requirements were met as follows :—

(*a.*) *Exposure and Division.*—The muscles were rapidly exposed over the dorso-lumbar region, and then partially extirpated and cleared from the vertebral laminæ ; hæmorrhage was treated by frequent irrigation with 0·6 per cent. saline at a temperature of 50° C., and pressure of hot sponges. The exposed vertebral arches were then carefully removed piecemeal for 6 to 8 centims., by the aid of powerful but fine-pointed bone forceps.

In those cases in which the reflex effects of the lower fragment of cord were investigated, the cord was only exposed for a very short distance by the removal of one lamina and then divided under profound anæsthesia. The small wound was then closed and kept covered with hot sponges.

When a long portion of the cord was exposed the theca was divided in the middle line with great care, the division being especially free at that portion of the exposed area which was to remain in continuity with an unexposed region, so as to avoid

any danger of strangulation when the freed portion of cord was subsequently raised. On reflection of the dura, a ligature was cautiously passed around one end of the exposed cord, the end chosen varying in accordance as it was desired that the observed portion of cord should be in communication with the brain or with the sciatic nerves. If the former, then it was knotted gently round the lower end so as to securely close the vessels, and the cord divided immediately below the ligature. The (central) end was now raised by the ligature, and the nerve roots exposed and divided one by one until the whole portion of the exposed cord was freed from all attachment except at the upper end, where it was continuous with the central unexposed region. In the case of experiments upon the cord severed from the brain but in connection with the sciatic nerves, the ligature having been applied round the upper portion of the exposed tract, the cord was divided on the central side of the ligature and the exposed portion freed downwards in a similar manner to that just described.

(*b.*) *Preservation of Circulation.*—The circulation in the exposed portion was maintained as far as possible by the ligature of its cut end, including the main vessels, and by keeping the cord in connection with an undisturbed portion, and avoiding any strangulation of that connection.

(*c.*) *The Immobilisation of the Spinal Column.*—The fundamental importance of fixing the vertebræ necessitated the employment of a special clamp. This clamp was applied so as to firmly grasp in its powerful vice-jaws the transverse processes of the spinal column in the immediate neighbourhood of the exposed cord. The jaws were fixed on a stem, and approximated by an ordinary double screw. In order to avoid the extraneous electrical effects which the presence of metal surfaces in contact with moist cut tissues necessarily involves, the jaws were made of stout pieces of ivory. The stem carrying them was fixed to a powerful upright attached to the experimental table, and so arranged as to secure a fixation vertically above the preparation. (See Plate 29.)

(*d.*) *Cooling and Drying.*—The exposed cord was kept bathed with the warm saline solution until it was actually the subject of experiment, when, if it were raised in air, care was taken to keep steaming sponges in its immediate neighbourhood.

(*e.*) *Isolation.*—The necessity of isolation for purposes of galvanometric observation will be referred to later on. This isolation was produced by raising the ligatured end of the exposed portion of cord, so that the portion swung in air without pulling upon its deep attachment. The electrodes, &c., were adjusted as described in the succeeding sections.

4. *Division of the Exposed Portion of Cord by a Longitudinal Incision.*

For certain purposes it was desirable to observe the galvanometric effects in each half of the cord independently. These were (1) the determination of the comparative

value of the cord excitatory effect direct and crossed when the cortex is excited, (2) the determination of the bilaterality of representation in one hemisphere, and (3) that of the extent to which fibres cross from one side of the cord to the other.

We therefore devised the plan of dividing the exposed portion of cord by a longitudinal incision, either in the lateral or antero-posterior direction.

The former was effected as follows :—

The cord, having been exposed, was severed, freed from its attachments, as previously described, but not ligatured. It was then kept bathed with warm saline, and placed upon a thin sheet of warmed cork with a shallow groove in it. The posterior fissure could always be easily seen, and a longitudinal incision was then carried through it from the posterior to the anterior fissure by means of a razor or sharp scalpel, the incision commencing at the attached end of the cord. It is essential that in this operation the instrument should neither pull nor press upon the cord unduly, but, since the division involves both pressure and pull, the infliction of injury can only be mitigated by slowly making drawing incisions, first only through the posterior fissure, and subsequently deeper and deeper until they have passed into the thickness of the cord. The exposed portion is partly divided in this way down to its point of transverse division for a distance of 2 centims. or more. Irrigation with warm saline being maintained, the edges of the wound are gently separated, when the central canal of the cord will be seen in the bottom of the cut; with this as a guide, it is easy to continue by similar incisions the mesial division, until a complete separation of the cord into two halves is effected. (See Plates 31 and 33.)

Each half thus prepared was now ligatured close to its cross section, and raised in air for the necessary isolation when it was desired to subject them to electrical observation. They were kept apart by the ligatures being carried to the respective ends of a glass T-piece, or of two vulcanite rods arranged as a V.

Frequently the cord, when thus prepared, bled rather freely from the central end of the cut.

The simplest way to check this was found to be to press into the lips of the cut a small fragment of soft dry amadou, and leave it in contact with the bleeding point.

It might, perhaps, have been expected that such division would seriously impair the physiological conduction of its fibres. It will be seen in the following pages that, as far as the lateral tract is concerned, such impairment is not evidenced by our observations, but that undoubtedly the posterior columns in the immediate neighbourhood of the incision are injuriously affected by the process.

We have also divided the cord into a posterior and anterior half by gently raising it when freed and passing through it a thin-bladed knife from side to side opposite the attachment of the ligamentum denticulatum, and carrying it forward to the free end of the preparation.

5. *Preparation of the Spinal Cord for Excitation.*

Another mode of preparation remains to be referred to, that, namely, in which the cord, when severed from its connection with the brain in order to investigate the functions of the lower fragment, is to be excited.

It was necessary for these experiments to sever the cord as high as possible, though, as a matter of fact, it was found advisable not to perform the operation at a higher level than that of the 7th dorsal vertebra, otherwise, serious impairment of respiratory and vaso-motor functions followed, and profound shock vitiated the experimental results. When the upper end of the lower fragment of cord was to be excited, this was further exposed, and a piece 5 mm. in length excised on the peripheral side of the section, so that by looking into the gap the structures on the cut surface of the cord could be seen and the excitation localised. The gap was made absolutely dry with amadou and small pieces of sponge when the cord was to be excited.

Finally, a series of experiments involved the division of the cord at two levels. A portion was thus cut off, both from the brain and from the lumbar plexus, and prepared so that one end could be connected with the non-polarisable electrodes and observed whilst the other was excited. In all these cases the upper division was effected first, so as to diminish the shock which the further operative procedure connected with the lower division caused. The end with which it was desired to connect the electrodes was then carefully exposed, ligatured and freed from its connections, as already described under (3), whilst the other end was prepared for excitation.

6. *Preparation of the Roots of the Nerves.*

The posterior and anterior roots were in some instances prepared for excitation, in others for observation. In both cases the roots chosen were those forming the *cauda equina*, and they were exposed by a suitable opening of the spinal canal and theca in the manner previously indicated. The roots were carefully separated and when required each one was ligatured near its peripheral attachment and divided. Great care is necessary to avoid pulling, drying, &c., in the case of the roots. (See Plates 34 and 35.)

7. *Section of Columns of the Cord.*

In many experiments it was necessary to make a section of one or more of the columns of the cord between the part excited and the part observed. The method employed was to expose a portion of cord for the purpose and then to make the section by means of Beer's cataract knife, completing it by means of a fine-cutting needle or occasionally fine-pointed sharp scissors. In every case the limitation of the section was ascertained by *post mortem* examination. When a hemisection of the cord

was to be made, an additional precaution was adopted to ensure its accuracy, the cord being fixed by a fine needle.

In some instances it was desirable that such intervening localised sections* should be made some weeks previous to the actual experiments. This notably increased the labour of the research, but is an essential control to such an experimental enquiry as the present one. The animal was in all instances etherised and the seat of operation having been carefully shaved, disinfected, &c., the necessary exposure and section were then made under all aseptic precautions; the wound uniting by first intention when treated in the manner described by one of us in previous experiments of this kind.

In conclusion, it may be pointed out that since almost each experiment involved exposure, &c., of several different portions of the central nervous system, we adopted the plan of performing these slowly, taking at least an hour or more in the preliminary operative part of the experiment. We found that in this way less general shock occurred than when the various parts were rapidly prepared one after the other.

Section 3.—Recording and Exciting Apparatus.

The recording and exciting apparatus used in the present research was chiefly that adapted for determining the comparative amounts of the electrical changes in the spinal cord and nerves at rest and when subjected to an excitation of definite intensity and duration.

The apparatus and its arrangement will be best indicated by separating it into the following groups:—

(1.) The apparatus used in connection with the observation of the electrical changes.

(2.) The apparatus used in connection with the excitation.

(3.) Extra apparatus used for determining the characters of the muscular contractions.

1. *The Electrical Apparatus for Observation.*

Both these instruments were used to indicate the electrical changes evoked in the spinal cord and nerves.

(*a.*) The *capillary electrometer* was made by Mr. G. J. Burch.† The mercurial column was magnified about 300 times by the special microscopic arrangement employed, and was sufficiently sensitive to show perceptible movements when connected with a difference of potential of $\frac{1}{10000}$ Daniell; its reaction was quick enough to enable it to respond to a difference of $\frac{2}{1000}$ Daniell when connected with that

* The localisation of all points or regions of the cord exposed is expressed in terms of the body of the vertebra, or intervertebral disc, opposite to which the section was made. We furnish in Appendix A the topographical relations which the spinal segments bear to the superficial origins of the several nerves from the spinal cord.

† Proceedings of the Royal Society.

difference by means of a rheotome for only $\frac{1}{1000}$ second. The ocular of the microscope was fitted with one of ZEISS's micrometers, the scale being worked across the field by a screw mechanism. In the particular arrangement employed, the scale bore such a relation to the actual dimensions of the capillary that one division corresponded to $\frac{4}{1000}$ millimetre of the object. A difference of potential of $\frac{1}{1000}$ Daniell when connected with the poles of the electrometer produced a movement of the mercury amounting to $\frac{2}{100}$ millimetre, and this, when viewed by means of the eyepiece, amounted to five divisions of the scale.

The element of uncertainty in connection with the movement of the electrometer under different conditions and the difficulty of obtaining reliable records of changes differing from one another by constant but small amounts, induced us to abandon the instrument for the quantitative observations which make up the bulk of the present research. It was, however, often used as a means of ascertaining the existence and character of electrical changes during the initial stages of a new series of experiments, and proved in this respect a useful guide.

The movements of the meniscus were in most cases observed by the eye, but in some cases they were photographed upon a travelling sensitive plate, as in the experiments described in our previous publication.

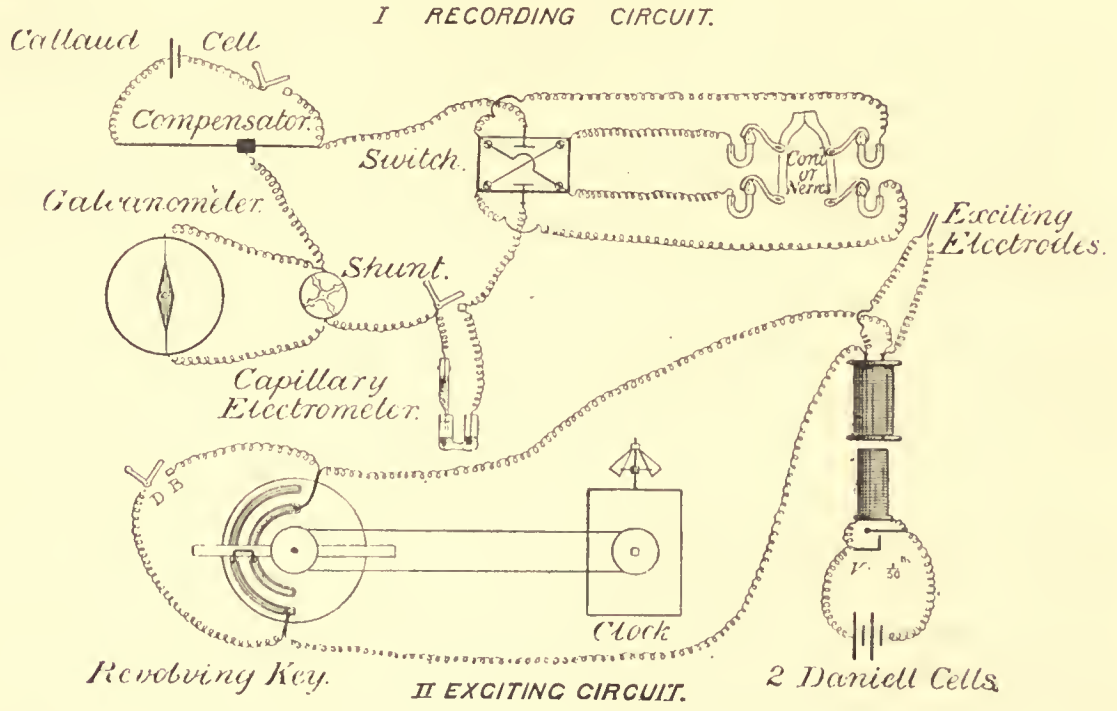
(*b*.) The *galvanometer* was the instrument upon which we relied for results susceptible of quantitative comparison. It was made by Messrs. ELLIOTT upon the lines of THOMSON'S reflecting instrument, and had a resistance at 16° C. of 20,364 ohms. The light magnetic system was effectually damped by being enclosed between two plates of glass 2 mm. apart, the aluminium vane of the ordinary Thomson being dispensed with to secure a decrease in the inertia of the system.

The degree of sensibility employed was such that the needle and mirror gave a deflection amounting by the reflecting method of observation used to 650 scale, when the instrument was connected through a resistance of 10,000 ohms (external to its own resistance) with a difference of potential amounting to ·01 Daniell, and when only $\frac{1}{100}$ of the current in the circuit was allowed by the shunt to traverse the instrument. The small mass of the system enabled it to respond to currents of very short duration, thus with an additional resistance of 10,000 ohms in the circuit, a difference of ·01 Daniell produced a deflection of 5 scale when connected by means of a rheotome with the galvanometer for a period of only $\frac{1}{1000}$ second.

The deflections of the magnetic system were measured by the usual reflecting method; a biconvex lens of 4 inches focal length was, however, introduced almost 3 centims. in front of the source of light between it and the concave mirror (of 40 inches radius) of the system. The screen behind which the light was placed was pierced by a circular aperture bisected by a vertical cross wire, and the reflected image on the scale was thus a large well-illuminated disc with a sharply-defined vertical shadow dividing it. The position of the edge of the vertical shadow on the scale could be thus observed with great accuracy, since the moving illuminated disc

was of sufficient size to embrace in its field a considerable range of the figures of the darkened scale on each side of the shadow of the upright.

Fig. 1.



The arrangement by which either of the above-described instruments could be connected with the experimental circuit, and thus with the particular structure, whether spinal cord or nerve, under investigation, is shown in fig. 1.

In the above arrangement the method of compensation and the method of connection with the tissues call for a few descriptive details.

(c.) The *compensator* was of the pattern used in the Physiological Laboratory, Oxford, and was similar in its general plan to that described by Burdon Sanderson, as used in his work on the electrical properties of *Dionæa*.*

The total amount of wire in the instrument offered a resistance of 10 ohms, of this a portion at one end, 125 centims. in length and of 1 ohm resistance, was exposed and lay tightly stretched upon a boxwood scale. Upon this boxwood bed a heavy block carrying a wire was allowed to slide. The block was furnished with a pointed index, the under surface of which, covered with platinum, formed the sole contact with the wire; its position was easily read upon the scale beneath it.

The battery used in the primary circuit of the compensator was the Callaud pattern, which is a Raoult battery without any porous cell. This had been found by one of us to be the simplest and most satisfactory battery for the purpose. As used in the present research, it consisted of a glass jar containing about a litre, into this

* 'Phil. Trans.,' 1882.

about 300 grms. of sulphate of copper crystals were placed, and the whole filled up with distilled water; a coil of sheet copper, with insulated connections, is immersed in the crystals, and a ring of zinc in the superficial liquid.

The cell was always prepared forty-eight hours before use, and since the subsequent alterations take place with great regularity and are slowly produced, the cell, when evaporation is prevented, is very steady, and is thus particularly suitable for the purpose indicated.

The value of a given interval between different points of the compensator wire when the Callaud cell was coupled up with it was always estimated before each experiment and contrasted with that produced by a known fraction of a carefully prepared Daniell cell. This latter was determined by the balancing method employed by DU BOIS-REYMOND and described by him in connection with his use of the "Rund Compensator" in his standard work on the technique of physiological experiments involving observations of electromotive changes. The measurements by the compensator, although made with the Callaud, were thus all translated into terms of a Daniell cell.

(*d.*) The *non-polarisable electrodes* which formed the connection with the tissues consisted in some instances of two pairs. Each pair was then joined to the two screws on one end of a Pohl's reverser (without cross-wires) to the middle screws of which the wires forming the main circuit were connected. Either pair of electrodes could thus be rapidly connected with the recording instrument by turning over the switch. In this way the changes in each of the two prepared sciatic nerves, or in each separated half of the isolated and longitudinally divided cord, could be ascertained one after another in rapid succession.

In the majority of experiments only one structure was examined, and one pair of electrodes was therefore used and introduced into the main circuit.

Each electrode consisted of a U-shaped glass tube containing a saturated solution of zinc sulphate with a well amalgamated and annealed zinc dipping into one limb. This form was preferred in consideration of the experimental necessity of keeping the electrodes exposed for an hour or more, in order to minimize the alterations due to evaporation.

It was of the first importance that the connection of the electrode with the investigated structure should be so firmly attached as to suffer no displacement from any chance movement of the animal, and that they should be of such a nature as to readily permit an adequate isolation of the structure from all its neighbouring tissues. This was effected in the case of each electrode by means of thread cables made out of the soft strands of such wicks as are used in ordinary paraffin lamps, since these readily imbibe and become soaked with moisture. Two strands 10 centims. long, were usually taken and soaked in 0·6 per cent. solution of NaCl; they were then plastered with powdered kaolin, made into a paste in similar liquid, and thus united into a double cable. This cable was passed under the structure investigated and tied gently

round it; the two ends of the tie were then united together, thus forming a cable of four strands. The end of this cable was fixed into a plug of kaolin moistened with similar sodium chloride solution, which was united in the usual way with sulphate of zinc kaolin paste, and this with the liquid in the one end of the U-tube. Since from 4 to 5 centims. of this yielding cable thus hung between the rigid part of the electrode and the attached structure, this latter could be moved so as to isolate it from the neighbouring tissues without interfering with its electrode connection, whilst, owing to the soft cable being tied around the structure no displacement of the point of contact was possible in consequence of such movement.

2. *The Exciting Arrangements.*

The method of excitation involved the use of (*a*) electrical, (*b*) mechanical, (*c*) chemical stimuli. Of these the electrical, as alone admitting of accurate graduation, is the most important.

(*a.*) *Electrical Excitation.*—The exciting arrangement involved in almost all cases the production of a rapid succession of induction shocks. These were obtained from the secondary coil of an induction apparatus of the general pattern of that devised by DU BOIS-REYMOND, and usually employed in physiological research. The particular coil used was made and standardised in Berne, under Professor KRONECKER'S direction, and differed from those ordinarily used in having a scale which denoted for every position of the secondary coil, with reference to the primary, the relative intensity of the current induction effect. (BOWDITCH.) Since the ordinary scale, that of distance in centims. is most generally known to physiological workers, we append the comparison of the numbers of the two systems showing their relative intensity.

Du Bois-Reymond inductorium scale.

cm.	0.	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.	16.	17.	18.	19.	20.	21.	22.	23.	24.	25
Divisions of Kronecker inductorium scale.	13,000	12,500	12,000	11,250	10,270	9,250	8,500	7,300	6,300	5,300	4,300	3,300	2,400	1,700	1,000	600	420	300	250	180	130	87	70	58	48	41
																Fraction over										

Two Daniell cells coupled for intensity were used in the circuit of the primary induction coil; this contained an automatic electro-magnetic vibrator, which closed and opened the circuit 50 times per second.

The interrupted circuit was a derivation bridging the primary coil (Helmholtz side-wire), so that each interruption should induce make and break currents of approximately equal intensity, thus avoiding the accumulation of polarisation after-effects in the excited tissue. The electrodes were well insulated platinum wires with points 1 millim. apart. When placed on the tip of the tongue, a slight acidity only was

perceptible with the secondary coil at 2000, the tingling effect becoming first distinctly felt at 4000, and painful at 12,000.

The arrangement of the exciting circuit is given in the preceding figure 1, p. 289, the only feature calling for remark being the use of a revolving mercurial key in the secondary circuit.

This key consisted of a hard paraffin bed, supporting two semi-circular narrow vulcanite troughs containing mercury. Into these dipped the two ends of a loop of stout platinum wire, which was carried by a horizontal revolving vulcanite arm. Each mercurial pool was connected with one terminal of the secondary induction coil, so that when the platinum loop connected the two pools a short circuit was made for the secondary coil. The arm was driven by a clock at such a rate that a whole revolution occupied a period of 10 seconds.

By means of the key (*D.B.*) shown in the plan, the secondary coil was additionally short-circuited, and the revolution of the arm thus made ineffectual ; when, however, it was desired to excite the preparation, the key was opened for one revolution only, and the secondary coil was thus disconnected from any short circuitous arrangement during 5 seconds. The interrupted induction currents were thus allowed to traverse the tissue between the platinum points of the exciting electrodes for this period only.

(*b.*) *Mechanical stimulation.*—The importance of obtaining evidence of physiological effects by different methods, as a control to the definite results obtained with electrical excitation, led us to employ mechanical stimulation wherever practicable. The simplest form of mechanical stimulus, and the most effectual, is undoubtedly that obtained by the complete and sudden severance of a tract of fibres. This we accomplished, when the position of the parts allowed of it, by the use of sharp scissors, thus severing, for instance, the sciatic nerve, and observing the electrical change which the division evoked in the spinal cord, and *vice versâ*. As, however, in some cases the metal blades of the instrument coming into contact with the moist tissue caused localised electrical changes, derivations from which affected the galvanometer and electrometer, we substituted the stimulus occasioned by the sudden tightening of a ligature, and also that caused by crimping the tissue, nerve, or cord, by squeezing it suddenly (sometimes so as to divide it) between the jaws of a pair of specially constructed ivory scissors.

The method of stimulus being used only as a control, the disadvantage of few repetitions being possible was not a serious one.

(*c.*) *Chemical Excitation.*—In addition to the previous methods of excitation, we have made use of strychnia, in intraperitoneal injections, in order to obtain pronounced reflex discharges from the spinal cord.

Further, we have frequently employed, with notable advantage, the method of exciting the brain first investigated by MAGNAN, viz., the production of nerve impulses from central apparatuses by the toxic influence of certain substances, especially the essence of absinthe.

Just as the mechanical stimulus affords, perhaps, the best control of the electrical stimulation of fibres, so the chemical, since it excites centres powerfully, affords a means of producing electrical changes in the efferent fibres from such centres which cannot possibly be due to actual escape of the exciting current.

For the performance of this method we have prepared the cord or nerve for connection with the non-polarisable electrodes as described previously, and then exposed for a short distance the external jugular vein, applying a small clip to the latter.

Two minims of the essence of absinthe were then injected with a hypodermic syringe inserted through the vein wall into the freely flowing blood stream.

The animal was then carefully observed and the first twitching indicating the commencement of a cortical discharge noted. It coincided in time with the beginning of large electrical effects as evidenced in the galvanometer. For further facts relating to this method we would direct attention to the Chapter dealing specially with the results thus obtained, *vide* p. 511.

3. *Extra Apparatus.*

The apparatus used for investigating the muscular changes evoked by excitation of the central nervous system was either adapted for a direct record of the character of the muscular contraction or for ascertaining the moment of its commencement.

When necessary the muscular contractions, whether evoked by cortical or spinal excitation, were recorded by means of a spring lever, made on the pattern of that employed by FICK for obtaining isometric muscular effects. The muscle was attached so that any changes in its tension were communicated to the spring, the small movements of which were magnified fifty times by a lever attached to its end. The lever recorded its movements on the blackened paper of an ordinary drum driven regularly by a clock.

When it was desired to ascertain the moment of the commencement of the muscular contraction, however evoked, the method employed by TIGERSTEDT was used. The Mammalian muscle was attached to the light "*unterbrecher*," which carried a weight of 10 grm. placed upon its axle, to ensure a steady pull upon the large muscle and a proper tension of its attachment. The *unterbrecher*, as in TIGERSTEDT'S method, formed a key in a separate circuit, which included a battery of three Grove's cells and one of SMITH'S* new electromagnetic signals. The break of the key and the consequent movement of the signal was recorded upon the glass plate of a spring myograph (DU BOIS-REYMOND'S *Federmyographion*) which travelled at a rate of 2 centims. in $\frac{1}{100}$ second.

* 'Philosophical Magazine,' 1889.

Section 4.—The General Procedure and the Precautions used by the Authors.

A. The Method of Experiment.

In any individual experiment in which excitatory electrical changes were observed the procedure we adopted was as follows:—

The animal having been anæsthetised and immobilised, the structure to be investigated was exposed and prepared in the manner indicated. It was always, whether spinal cord or nerve, divided, and the soft cables of the non-polarisable electrodes were then tied, one round the structure close to the point of division, the other about 1 centim. away round the surface. The ligature upon the cut end enabled this portion of the tissue to be suspended with its cables in air, without dragging on the remaining portion of the tissue which remained *in situ*. The cables were then connected with the non-polarisable electrodes. (See Plate 29.)

The electrical difference between the two contacts was first observed and balanced by the introduction by means of the compensator of a suitable difference opposite in sign to the tissue difference. The general characters of the latter and the amount of the balancing difference were then noted, both the galvanometer and electrometer being used for this purpose.

One of us devoted himself to the observation and record of the electrical changes; the other to the maintenance of the animal in a uniform condition of anæsthesia, to the prevention of the drying, &c., of the investigated tissues, to the observation of the muscular contractions, and to the excitation.

The tissue to be excited, which had been exposed with that under investigation, was then finally prepared, and the points of the electrodes were brought into contact with it under all the precautions to be immediately described.

The electrodes were kept short circuited as already stated by means of a key under the control of the observer at the galvanometer, &c. When everything appeared favourable and the galvanometer needle had been brought to its zero position by suitable compensation the revolving exciting key was set going and the control key opened for one revolution of the revolver; an excitation of definite duration and intensity was thus applied to the excited tract, whether cortex, corona radiata, spinal cord, or nerve. The extent of any deflection of the galvanometer needle or the movement of the meniscus of the mercurial column was noted, and special attention paid to its character. The extent recorded was always that between the previous resting position and the point where the moving recorder, whether spot of light or image of meniscus, stopped and commenced its return. If no return occurred but only a deflection produced which continued to creep on then the observation was disregarded as worthless. Such an effect was found to be generally associated with some movement of the animal which caused a slight displacement of the electrode contact.

Whilst one observer noted the electrical effect, the other noted the extent and character of any muscular movements by which the animal responded to the stimulus.

It need scarcely be said that the whole method involves the use of special precautions to avoid the introduction of fallacious and misleading effects, especially when it is desired to obtain a succession of results which will admit of quantitative comparison.

These precautions are, in the opinion of the authors, of the utmost importance and must be considered in some detail.

B. Precautions in Connection with the Method.

The special precautions may be grouped as follows :—

(1.) Those connected with the isolation of the particular region under observation.
(2.) Those connected with the condition of the non-polarisable electrodes.
(3.) Those connected with the condition of the animal.
(4.) Those connected with the localisation, &c., of the excitation.

(1.) *The Isolation of the Particular Region Observed.*

It is, in our opinion, an essential condition for the accurate employment of any method of localisation which relies upon the evidence of electrical changes in a given region, that the region in question should be as far as possible isolated. In the galvanometric experiments alluded to in the History (p. 279), as carried out upon the cerebral hemispheres, such isolation was not affected; a door was thus left open for introduction of errors which it is not easy to control.

We have repeatedly had occasion to observe that when a pair of non-polarisable electrodes is placed upon the cord lying *in situ*, or upon the surface of the exposed brain (see fig. 26, Chapter XI.) electrical differences present themselves and influence the galvanometer, this being evidently due to the fact that the parts with which the contacts are made, since they form one directly continuous mass with the structures around them, lie in the path of the derivations of currents, whose primary electromotive source is far removed from the electrodes.

In this connection we may refer to the derivations of the electrical difference between the different regions of the beating* heart which are present in the body.

On connecting two points on the surface of the exposed brain by means of non-polarisable electrodes with the galvanometer, any reflex movement of the scalp muscles lying outside the exposed region was found to evoke electrical changes in the points of contact, and if structures so far removed from the seat of observation can affect the contacts, how much more easily will these be affected by sources of electromotive differences situated in the deeper fibres, &c., of the brain. The fact that electrical

* Waller, 'Phil. Trans.'

changes manifest themselves between two surface contacts is thus by itself no proof that these electrical changes have their source in the tissue in the immediate neighbourhood of the contacts. It is, however, easy to ascertain whether the opposite conclusion is or is not true, by slicing off the two portions of the surface to which the electrodes have been attached, destroying their vitality, and replacing them in contact with the subjacent tissues, so as to act as mere moist conductors. If under these circumstances electrical changes are observed in the electrode areas, then it is clear that since all structural and physiological continuity is destroyed, these changes must be due either to (1) physical properties of the observed region, which are in no way associated with physiological vital changes; or (2) to the physical spread of derived currents from electrical changes of physiological origin in the deeper uninjured tissues.

The further distinction between these two alternative causes is effected by observing to what extent the electrical changes disappear in consequence of systemic death, since this obviously will affect the second class but not the first.

It is, in our opinion, essential in all exact experimental investigations carried out upon a particular region of such a mass of conducting material, as the body of an animal constitutes, to use a method which can by strict investigation carried out along the above lines be shown to exclude such discrepancies.

It may be pointed out that whilst we have selected the brain mass as a typical instance, the same objections apply with equal or greater force to the investigations of the spinal cord *in situ*. When it is remembered that the exposed cord lying in its cavity is brought into immediate connection with a large mass of muscles, some uninjured, some cut for operative purposes, and with the whole contents of the abdominal and thoracic cavities, it is not to be wondered at that the slightest movement of the animal should cause very large electrical changes between any two portions of the surface of the exposed cord, these being simply due to an alteration in the position of muscles or other structures, all of which are the seat of electromotive change. Such alterations must seriously influence the particular effect which may manifest itself when any two portions of the exposed cord are connected with the galvanometer. The force of these considerations is strengthened when it is borne in mind that the particular effects which the electrical method is to gauge, are excitatory in character. Of what value would any excitatory effect be, if, when it is evoked, there are, as is almost always the case, not only marked excitatory electrical changes in other organs, muscles, &c., but general movements and displacement of subjacent parts as the result of the excitation?

Enough has now been said to point out the necessity for the utmost possible isolation of the observed region, if it is desired to ascertain by the electrical method the presence of electrical changes due to electromotive differences occurring in that region only, and which may be therefore interpreted as indicating the presence therein of excitatory conditions.

The most complete method of isolation is obviously the removal of the structure

under observation from all contact with other tissues. This is not possible in the case of the Mammalian central nervous system; it is, however, quite feasible in the case of the spinal cord to ensure an isolation which we find to be sufficient. This, as has been detailed in the section dealing with the operative procedure, as regards its essential feature consisted in always dividing the cord, freeing it for several centims. from all its attachments, ligaturing the divided end, and suspending this portion in air by means of the ligature (see Plate 29). The cord is thus only in connection with the structures by its deep end, and any spread of electrical currents, &c., which have their source in extraneous regions, can only occur in this portion of cord as "extrapolar effects"; further, the electrodes being placed one upon the extreme end (cross section), the other only half to one centim. on the proximal side of this, such extrapolar derivation effects, if present, must be still more diminished by the distance, 3 centims., between the electrode contacts and the deep connections of the cord.

The necessity of the above careful isolation has been impressed upon us by the ease with which it is possible to introduce errors even where this mode of connection is carried out. If, for instance, either the proximal contact be allowed to slip down and to approach too closely (within 1 centim. or less) to the deep structure, or if the latter, by the presence of large quantities of liquid, &c., be brought into connection with a portion of the isolated tract close to the proximal electrode, then, even with the remaining electrode contact well isolated, electrical effects manifest themselves between the contacts, which we have no doubt are really due to extrapolar spread from changes in the deeper tissues. Thus, for instance, the anterior roots, even when divided and one end isolated, present great difficulties, owing to the shortness of the tract intervening between the contacts upon them and the cord from which they spring. Electrical excitatory effects can be obtained on exciting the brain, which are apparently situated in the anterior roots, but which are in this arrangement largely due to electrical changes, situated in the cord, and occur as extrapolar derivations in the anterior root. This is readily proved by using the method of control previously referred to, viz., cutting off the attachment of the root to the cord and then replacing it in its old position, when, in spite of the want of structural and physiological continuity, the changes are still found to occur.

We cannot lay too much stress on the necessity of careful isolation as far as practicable, and of careful investigation by both the methods indicated, and other similar ones, of the extent to which observed electrical effects are due to mere physical spread through the moist tissues of changes in other regions than the observed ones.

It will be understood, therefore, that in the following experiments, when the cord or sciatic nerve was observed, the length of the tissue afforded every facility for placing the electrode connections at a safe distance from the point where each of these structures came into relation with the general mass of the body, and in consequence a position could be chosen in which all danger of extrapolar spread might with ordinary care be guarded against. When, however, the roots were observed, since

the distance in question was necessarily short, the dangers of extrapolar spread were increased, and the experimental results had to be controlled with great care; this danger was most formidable in the case of the anterior root, as owing to its anatomical relations it could not be so conveniently separated from its contiguity with the mass of the cord, and the errors thus introduced have been at present sufficiently serious for us to abandon these roots for direct connection with the galvanometer, and rely on those experiments performed upon the sciatic nerve with all the posterior roots cut.

(2.) *The Condition of the Non-polarisable Electrodes.*

It is scarcely necessary to observe that one obvious precaution in connection with the electrodes is to ascertain, before commencing the experiment, that between the electrodes themselves there is only an extremely slight and constant electrical difference, and noting its amount in terms of the compensator.

There is one difficulty, however, which appears to be inseparable from a method which involves a long bridge of kaolin moistened with 0·6 per cent. of saline, exposed to the air of the room, and that is the alteration of resistance due to slow evaporation. This alteration does not affect the results when observed by the electrometer, owing to the very high resistance offered by the latter. It may, however, seriously affect the galvanometer results. It will be obviously mitigated by employing a circuit of very high resistance, and this we always took care to do, the full resistance of galvanometer and electrodes amounting to little short of 50,000 ohms.

It is, however, necessary to keep in mind the presence of such alterations, and to ascertain by repeated measurement of the galvanometric effect produced by a given difference in the compensation circuit, whether the resistance has so altered as to vitiate the value of the results. Where experiments follow one another closely, as was the case in all the instances in which the different columns of the spinal cord were excited, any alteration would be obviously too slight to exercise an appreciable influence upon the results, which admit, therefore, as far as this feature is concerned, of strict quantitative comparison.

It is obvious that remoistening of the electrodes must only be effected at the commencement of a fresh series of observations, and must on no account take place during any given series.

(3.) *The Condition of the Animal.*

(*a.*) *General Preliminary Condition.*—In all the experiments this was a very important factor, which we early recognised as determining the success or failure of the particular observations. If the animal were ill, or had been much exhausted by the preliminary anæsthetisation, &c., it was noted that the electrical changes, whether due to currents of rest or of action, in both nerve and spinal cord were comparatively small in amount. This was especially the case in the Monkey.

(*b.*) *Anæsthesia.*—The degree of narcosis is an extremely important factor. It will

be seen in the chapters which deal with the different groups of results, how the effects obtained in slight anæsthesia differ from those obtained with similar stimulation in profound narcosis. It was, therefore, extremely important to keep the condition of anæsthesia as far as possible even, and to note as a guide to that condition the presence or absence of muscular movements, when any part of the central nervous system was stimulated.

In one respect, the degree of etherisation was most useful, since it served as a valuable control against error due to simple electrical escape from the exciting into the galvanometric circuit. It is evident, if on pushing the degree of narcosis the electrical changes in the observed tissue are very much diminished or even abolished, whilst the excitation by electrical current remains unaltered, that no physical conduction of derivation currents from the exciting into the galvanometric circuit can be present.

(*c.*) *Collapse.*—Since the experiments are often necessarily spread over a considerable period of time, the gradual collapse of the animal is not infrequent. Its onset is readily distinguished, and can be allowed for by diminishing the amount of etherisation (see p. 282), and by increasing the intensity of the stimulus used.

(*d.*) *Hyperexcitability.*—In connection with this part of the subject must be noted the variations in excitability of parts due to section.

As regards the cortex it has occasionally happened that it has been slightly punctured by an electrode point, &c. Whenever this happened the effect was to heighten the excitability of the immediate neighbourhood, and to produce thereby a very marked epileptogenous change. A more extensive injury has the further effect of abrogating not only this increase of excitability, but the normal degree as well.

As is well known, the excitability of nerve *fibres* is raised by their section, and from a rapidly attained acme the excitability steadily diminishes, passing the normal point and becoming subnormal. François Franck has shown the same to be true for the reflex centres in the spinal cord, when division of the latter has been carefully made high up and without notable hæmorrhage. We have always borne this in mind, and have discounted the rise and fall of excitability due to the section in each observation.

(4.) *Localisation of the Excitation, &c.*

Many precautions had to be observed in carrying out the stimulation of the cortex, spinal cord, and nerves respectively, especially when the excitation of these structures was electrical.

A. *Cortex.*—As previously stated, it was, of course, found imperatively necessary to keep the surface of the cortex both warm and moist, this being especially achieved by replacing the skin and by irrigation with warm saline solution. To avoid short circuiting and consequent irregular intensity of the exciting stimulus, the surface of the brain was always carefully dried with soft sponge or amadou immediately before

the application of the electrodes. Fatigue of the cortex was avoided by suitable intervals of rest.

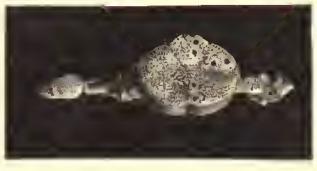
The intensity and character of the stimulus is referred to under apparatus, p. 291, but it may be here stated that the electrodes were fine platinum points 1 to 2 mm. apart.

B. *Corona Radiata.*—To expose the corona radiata it was necessary to raise the cortex by a horizontal incision, and then to check the bleeding from the pial vessels with pieces of amadou around the cut border of the area exposed. If after several excitations the exposure had lowered the excitability of the fibres, the electrode points were sometimes inserted 1 mm. deep into the substance of the corona, instead of, as usual, resting gently on the surface. The electrodes employed were the same as those for the cortex.

C. *Spinal Cord.*—The excitation of the spinal cord, especially for purposes of differentiation of the columns naturally demanded special attention. We obtained our initial generalisations by means of exciting needles fixed on either side of the cord or pressed against the longitudinal columns, *vide* pp. 369, &c.

This method we soon discarded (Section 6, Part V.,) for that now to be detailed, viz., the excitation of the cut sections of the columns of the cord, inasmuch as the differentiation of the bundles of fibres could thus be accomplished at the same time as other objects in view. The cord having been previously divided in the manner stated above, and the surface and surrounding tissues being carefully dried, the fine platinum electrodes, 1 mm. apart were used. It was our aim to provide for the excitation of as many fibres in any column as possible in order that the largest galvanometric effect might be evoked, and at the same time to avoid extrapolar excitation of neighbouring columns. These particulars were fulfilled by applying the two electrode points, as indicated on the accompanying fig. 2, *i.e.*, vertically on the anterior and posterior columns, and horizontally on the lateral column in the region of the crossed pyramidal tract.

Fig. 2.



Photograph of a transverse section of the fresh spinal cord (Cat) at the 7th dorsal nerve, slightly magnified. The remarkable differentiation of the posterior columns in this animal (Schiff) is well seen.

That these measures were effectual in localising the stimulus was demonstrated by the fact that the placing of the electrodes on the neighbouring sections of the grey columns evoked no electrical changes, as evidenced in the galvanometer connected either with the issuing nerves or with another portion of the cord; so that the

positive electrical results following stimulation of a column, the posterior, for instance, were to be attributed entirely to the localised stimulation of the structures upon which the points of the electrodes rested.

A further point is the special difficulty of maintaining the electrodes properly in position, *i.e.*, in contact with the cord, inasmuch as the spinal muscles on their contraction shake the cord a little, although the spine be fixed. This, of course, applies only to the end excited. Imperfect apposition of the electrodes was best avoided by holding them in the hand, the latter being suitably supported. As is described on p. 292, the duration of excitation was provided for by the revolving mercurial key; consequently, after the proper contacts had been made as above, each observation was comparable with another as regards the degree of the excitation. The important bearing this has on the quantitative value of the galvanometric readings is sufficiently obvious.

D. Nerve.—In electrical excitation of the nerve, we were chiefly anxious at first to avoid possibility of spread. Beginning with ordinary sheathed electrodes, into which the sciatic nerve was laid, we very soon laid these aside for the more accurate and simpler plan of applying platinum electrodes to the nerve raised in the air by a thread.

The mode of exciting a nerve in relation to its cross and long diameter respectively, has for some time been the object of research (Hermann, Bernstein, and others). Gad,* in referring to the action of carbonic acid, and especially of alcohol, on the excitability and conductivity of nerve fibres, raises this question again, and strengthens the fact that transverse excitation is much more adequate (5–6 times) than stimulation applied longitudinally. Apart from incidental polarisation it is clear that the larger number of fibres lying in the principal axis between the poles chiefly conditions the result.

To produce a maximal effect we have, therefore, always applied the platinum electrodes, so as to bend the nerve slightly between the terminal points. (See fig. 3.)

Fig. 3.

Inasmuch as we always sought to obtain, with as weak an excitation as possible, a maximal effect for purposes of quantitative as well as qualitative comparison, it was especially necessary for us to excite, without fail, all the fibres in the nerve.

The usual method of simply placing the nerve on the electrodes, as, for instance, in using sheathed or hook patterns, only enables a few fibres to be excited—those immediately in contact, or nearly so, with the metal. Thus, Beevor and Horsley†

* 'Archiv für Physiologie,' (du Bois Reymond). 1889, p. 350.

† 'Roy. Soc. Proc.,' 1888.

have seen differentiation of a mixed nerve on applying the electrodes to one or other side of the trunk of the hypoglossal above the descendens noni branch.

We have, of course, found that great differences are produced according to variations in the condition of the Mammalian nerve under varying circumstances.

The nerve must not be dragged upon in any way and the electrodes must be in good *moist* contact with the bared fibres, the intervention of fat or fascia or dried epineurium being sufficient to diminish or prevent the excitatory effect.

CHAPTER IV.—THE RESTING ELECTRICAL DIFFERENCE IN THE MAMMALIAN NERVE AND SPINAL CORD.

The experiments which form the subject of the succeeding sections furnished us with a large number of observations as to the amount and character of the persistent electromotive difference which exists in the Mammalian nerve and spinal cord between the cross section and surface.

The number alone of the experimental observations would be sufficient to warrant their introduction at this stage in a chapter devoted to their consideration only; but as in addition they seem to furnish valuable side evidence as to the relations of the spinal cord both to the cerebrum and the issuing nerves, such an exclusive study becomes a matter of necessity.

It is well known that when by means of appropriate contacts the cross section is compared with the longitudinal surface of a living nerve, an electromotive difference is found to exist, of such a character that if examined galvanometrically the surface is positive to the cross section. The current associated with this difference was termed by its discoverer, DU BOIS-REYMOND, the nerve current (*nervenstrom*), and by others, HERMANN, HERING, the demarcation current, since it is presumed by them to have its seat in the zone of tissue which at once bounds and divides the region of living from that of injured and dead or dying nerve. The use of either of these terms is, we consider, objectionable in the present instance, since our object is merely to state the actual fact without involving any cause thereof; we will therefore designate the persistent electrical difference just referred to the *resting difference*.

The difference was in all cases estimated in the following manner. By means of the long compensator, described in the preceding chapter on apparatus, a known difference of electrical potential was introduced into one part of the electrode circuit of a sign opposed to that present at the electrode contacts, and the former was then adjusted until the galvanometer showed no current to be present in the circuit; the original difference between the two electrode contacts is thus given in terms of decimal fractions of the constant external source of difference of potential. As already indicated, this source was the Callaud cell, the E.M.F. of which was itself estimated by a similar balancing method in terms of a carefully prepared Daniell cell.

The special structures investigated fall into three classes—

A. Sciatic nerve.
B. Posterior root.
C. Anterior root.
D. Spinal cord.

A. Sciatic Nerve.

1. *Amount of Difference.*

The resting difference between the cross section and the longitudinal surface of the Mammalian nerve was estimated by du Bois-Reymond as ·026 D. in the case of the Rabbit;* a much less marked difference, ·005 D., was observed by Israel† in the sciatic of the same animal. The amount of the difference in the sciatic nerve was observed in various Mammals by Fredericq,‡ who obtained the following results :—

Cat	·017 to ·018	Daniell.
Dog	·018 „ ·024	„
Rabbit . .	·015 „ ·028	„
Duck . . .	·024 „ ·026	„
Horse . . .	·004 „ ·007	„

Our own results were obtained with the Cat and Monkey. In all cases the sciatic nerve of the anæsthetised animal was exposed in the popliteal space, ligatured, and divided below the ligature.

The results obtained with 69 sciatic nerves in the Cat are given in Appendix B, I., these are separated into those in which the cord, and thus the nerve, was connected with the brain, and those in which the cord was divided. The average result of both sets is the same, being ·0094 Daniell in both. The influence of complete section of the nerve at the sciatic notch was also observed in some cases, and was found not to affect the amount of the difference for the first minute or two. The highest difference ever observed was Cat (70)§ and Cat (75), when it amounted to ·018 Daniell, the lowest was ·004. Whilst then the average amount is much lower than that which previous observers above referred to obtained in the Rabbit, the maximum corresponds to that noted by Fredericq in the Cat.

The results obtained in the case of the Monkey are shown in Appendix B, I. Twelve

* 'Gesammelte Abhandl.,' vol. 2, p. 250.

† Israel, 'Archiv f. Anat. u. Physiol.,' 1877 ('Physiol. Abth.,') p. 451.

‡ Fredericq, 'Archiv f. Anat. u. Physiol.,' 1880 ('Physiol. Abth.,') p. 65.

§ In all cases where a number in brackets follows the mention of an animal, *e.g.*, Cat (70), it refers to the page in our note ledger. The number of observations is so large that, for purposes of control and correction, we have been compelled to thus check the record.

nerves were examined and the average difference amounted to only ·005 Daniell, whilst the highest difference observed was ·007, and the lowest ·003. This diminution in the case of the Monkey cannot be attributed to the smaller size of the sciatic nerve in the common Macaque Monkey, which is generally experimented upon, since in two cases large Rhœsus Monkeys with big nerves were used, and in these (333), (368) the highest difference is ·007, and the average ·0055. (Compare the proportions of the nerves as shown in Plates 30–35.)

Moreover, as the previous results obtained by FREDERICQ show, the amount of the difference does not vary directly with the size of the nerve when different classes of animals are used, of which the high difference in the Rabbit and the low difference in the Horse is a notable illustration.

It will be seen that the spinal cord resting difference in the Cat and Monkey exhibits the same contrast as that of the sciatic nerves.

It has been stated that the resting difference in the nerve is not perceptibly affected by division of the spinal cord, when the division is carried out at the time of the observation. It appears, however, that section of the cord one to two months prior to the experiment does affect the amount of the difference. This influence, though small, seems to be sufficient to enable the observer to judge, when the cord lesion has been unilateral, upon which side it is situated.

Thus in an animal, Cat (227), in which the left lumbar posterior roots had been divided, the left nerve difference was ·007, that of the right ·009. In another animal, Cat (223), in which the right posterior column had been divided, the right nerve difference amounted to ·005, the left ·008, and in an animal (259) upon which a hemisection on the left side had been effected, the left nerve difference was ·007, the right ·008.

In one case after section of both posterior columns (Cat) the difference in each nerve was ·012, an amount which is somewhat in excess of the average.

2. *Alterations in the Resting Difference.*

The alterations in the difference occurring whilst the nerve was under observation may be divided into :—

(*a.*) Those due to physical changes, affecting the contacts and derivation currents, and due to loss of moisture from evaporation, change of temperature, &c.

(*b.*) Those only to be accounted for as connected with slow physiological changes in the tissue, the chief agent in such alteration being loss of vitality, due to arrest of the circulation, and to other causes.

(*c.*) Those directly connected with the production in the tissue of excitatory physiological processes.

We will now examine these separately in detail.

(*a.*) *Physical Changes.*—With regard to the effect of physical changes, such as

temperature, drying, &c., these influence the electrical resistance of the tissue surrounding by altering the moisture with which it is infiltrated. The result is to cause an alteration in the balance previously existing between the currents due to the tissue and the compensator source. The character of this will be made evident by citing a case.

The sciatic nerve, prepared as above, and hanging free in air, was connected by its cross section and surface with the galvanometer electrodes, the resting difference between the contacts was compensated at first by a difference of ·01 D. The nerve was then moistened between the contacts, this necessitating a reduction of the compensation to ·0085 D. This alteration is obviously due to the fact that the increased moisture has decreased the resistance in the surface of the nerve, and thereby increased the intensity of all currents which are present in that region. These currents are, first, a portion of the balancing current, and secondly, the derivation currents between the surface and cross section of the nerve. Whilst these two are equally affected between the points of contact of the electrodes, the result as regards the galvanometer circuit is very different. This will be rendered clear if we remember that the tissue difference is usually that obtained by connecting two surface points of a series of closed circuits, through which currents flow, and that the resistance of the circuits varies inversely with the amount of tissue moisture, so that the amount of spread, and thus the particular derivation on the surface, is diminished by the increased moisture. The final result is that, as regards the galvanometer circuit, there is now a current in the direction opposed to that due to the tissue difference, this being due to the over compensation, and rendered more distinct by the lessened resistance in the whole galvanometric circuit which the moistening involves.

The effect of drying must be the reverse of that indicated. It became noticeable in our prolonged experiments upon the Mammalian nerve and spinal cord, since it was essential for our purpose to perform the experiments in a room at about 70° F. As far as possible the errors due to this were obviated by the use of steaming sponges placed under the structures, but a slow steady rise in the amount of the difference during the first 5 or 10 minutes after the electrodes have been applied, and maintained unaltered, is usually seen in the cord, *vide infra*, and although not a very noticeable feature in nerve, may, when present, be partly attributed to this cause.

As just indicated the temperature was kept tolerably constant, but, as HERMANN and others have shown, the gradual rise in the temperature of the experimental room, may cause a similar slow increase in the amount of the difference. This alteration is, however, strictly of physiological origin, being related to a change in the molecular condition which lies at the foundation of the difference.

This brings us at once to the alterations which may be more especially ascribed to physiological changes.

(*b.*) *Slow Physiological Changes not Obviously Excitatory.*—The alterations of this kind in the resting difference due to physiological changes are in the case of nerve

usually a fall in the amount. Sometimes it has happened that a rapid rise for the first few minutes has been observed which did not admit of explanation as being caused by either of the two agents just indicated; and the presence of such a rise to a very marked degree in the case of the spinal cord as well as its presence in the isolated nerves and muscles of the Frog, renders it probable that in the Mammalian nerve, when present, its origin is physiological.

The fall is undoubtedly connected with loss of vitality, and may vary between the slow diminution which follows arrest of the circulation, and the rapid fall produced by injury of the nerve in immediate proximity to the surface contact.

The alterations which especially call for remark here are those which are entailed by the death of the animal on the one hand, and by the severance of the nerve from the spinal cord on the other. The first is probably due to several factors whilst the second is due both to arrest of the local circulation and the destruction of the continuity of the nerve fibres with their trophic centres in the cord.

In the case of the sciatic nerve, the alteration seemed to us to be the same in extent whichever event occurred; that is to say, the resting difference for the first 30 minutes slowly diminished in amount at the average rate of $\frac{1}{10000}$ Daniell per minute, this rate of diminution becoming less afterwards.

It is, however, questionable to what extent in the suspended and isolated nerve, the physiological conditions which are dependent upon continuity with the cord are maintained by any facilities which the preservation of vessels affords for keeping up a circulation in the nerve, since this must be, undoubtedly, greatly impaired by the exposure. The conditions of vitality would rather seem to be linked with the maintenance of physiological connection with other nerve structures, around which an active circulation is still being carried on, and which, therefore, retain their normal vital characteristics. That this is probable is shown by the fact that when, as sometimes occurs, the nerve difference, owing to rapid drying, shows a steady rise in amount, which rise continues even when no evidence of circulation in the exposed nerve is obvious, the rise is immediately counterbalanced and converted into a fall on systemic death of the animal, this fall occurring *pari passu* with the loss of excitability in the central nerve structures.

(*c.*) *Physiological Changes Connected with Excitation.*—The alterations due to excitation were after effects, that is, they followed the development of the transient excitatory change and consisted in a permanent slight diminution in the previously existing difference, such as has been observed to follow nerve excitation in the case of the Frog.

The slow after effect can be readily distinguished from the transient rapid electrical changes due to the actual presence of excitatory processes evoked by the application of the stimulus, since these are synchronous with the excitation, whereas the after-effect is very variable in its duration, but always follows cessation of the stimulus, and persists for many seconds.

We have noticed that it is more pronounced when the etherisation has become slight in degree.

In addition to the after-effect due to excitation there are seen under certain circumstances, particularly that of inadequate etherisation, changes in the nerve difference, which in the galvanometer indicate their presence by the needle now slowly rising 30 to 50 scale, and now falling. These disappear when the anæsthesia is rendered more profound, and are much more marked in the case of the spinal cord; they are probably due to the occasional discharge of groups of minimal nerve impulses, and are analogous to those first observed in the medulla of the Frog by SETSCHENOW.

B. POSTERIOR ROOT.

1. *Amount of Difference.*

We have made six experiments upon the posterior root. In these a lumbar posterior root was exposed, ligatured, and divided as close to the ganglion as possible, without involving this structure, and the root thus left connected with the cord was suspended in air by the attached thread. The particular root chosen in five cases was the 7th of the lumbar series, since this is the largest in the Cat of the roots forming the lumbar plexus (see Plate 35). The galvanometer electrodes were attached, as in the nerve, by means of thread cables moistened with ·6 per cent. NaCl, to the cross section and the longitudinal surface, and the amount of the resting difference determined by the balancing method.

The result in the five animals was found to be ·026, ·02, ·02, ·018, and ·016 Daniell respectively.

Hence although the 7th lumbar root is less than half the size of the sciatic nerve, the average amount of the resting difference, ·02, is about twice as large. (The 6th lumbar root was observed once, the difference being ·012.) This remarkable circumstance is very significant when the proximity of the structure to the spinal cord is taken into consideration, and deserves a more extended investigation. It may be pointed out that SCHIFF observed that there was a resting difference between contacts when placed upon a more central and a more distal portion of a continuous nerve, the central contact being positive to the other; also that excitation of any portion of the tract caused an excitatory change, in which the tissue under the first contact became galvanometrically negative to that under the second more remote one.

Further, both GRÜNHAGEN and BERNSTEIN have noticed that the central portions of the nerve are more excitable than the distal portions. Now whether the persistent difference be fundamentally the same in kind as the transient excitatory electrical change or not, there is an undoubted quantitative relationship subsisting between the two. It is, therefore, not surprising that there should be found an increase in the amount of the resting difference obtainable in the posterior roots as compared with the sciatic nerve.

2. *Alterations in Resting Difference.*

(*a.*) *Physical Changes.*—The alterations due to drying probably have the same influence as that already alluded to in the case of the sciatic nerve. The amount of the difference noticed immediately after section generally increases slowly and steadily, and, at least partially, from this cause. There is, however, a noticeable check in the rise after the first five minutes, after which the difference then only in some cases begins to fall. Hence either the rise is accentuated at first by some other agency, or it is counterbalanced by the depressant effects due to loss of vitality.

(*b.*) *Physiological Changes.*—The amount of the difference in the root diminishes with greater rapidity than in the case of the nerve trunk, in consequence of systemic death. A similar fall occurs if the root is severed from its central connection. This is illustrated by the following series of experimental observations made before and after the death of the animal.

Left 7th Lumbar Posterior Root.* (Cat, 362.)

Root Divided near Ganglion and Central End Connected with Electrodes.

	Time of observation.	Amount of difference.
	11.42	·019
Excitation experiments carried out .	11.45	·02
	11.51	·0195
	11.55	·019
Systemic death	12.0	
	12.3	·0185
	12.12	·018

Root cut off from Cord.

Time of observation.	Amount of difference.
12.13	·0175
12.14	·017
12.15	·016
12.16	·0155
12.18	·015

In another animal after systemic death had caused a decline in the amount of difference, severance of the root caused no further appreciable decline.

* See Plate 35.

The root, therefore, in this respect behaves, as far as these two experiments enable us to judge, like the nerve.

(c.) *Changes following Excitation.*—In consequence of either direct excitation of the root or its indirect excitation through the cord, the amount of the difference is decreased, an after-effect following the passing away of the true excitatory change similar in character to that seen in the nerve.

The rising and falling in the amount of the difference when the anæsthesia of the animal is not sufficiently profound is rather more marked in the case of the posterior root than in that of the mixed nerve.

C. Anterior Root.

With regard to the anterior roots, we have only performed one experiment. There are considerable difficulties in the way of connecting the anterior root satisfactorily with the electrodes, so as to exclude all possibility of obtaining results which are derived from electrical changes in the cord. These difficulties are mainly the shortness of the root and the characters of its anatomical relations with the cord, it being difficult to obtain a sufficient length. Moreover, our purpose being rather to obtain the evidence of excitatory than of resting electrical changes, the shortness of the root, when combined with the movements of the animal, caused serious errors in observation, due to the displacement of the electrodes and their being thus brought near to or in contact with surrounding structures. In the single case in which the 6th left lumbar anterior root was divided and its central end connected with the galvanometer electrodes, the difference (Cat) was found to be only ·0045 Daniell, whereas the 6th lumbar posterior root of the same side, when examined, showed a difference of ·012 Daniell.

D. Spinal Cord.

The fact that the cord exhibits, like the nerve, both a persistent difference between its longitudinal surface and its cross section and a true excitatory effect, was discovered by du Bois-Reymond, and has been since confirmed by other observers, notably Setschenow. The general features of the same were described by us in our preliminary communication made to the Royal Society, but a systematic analysis of a number of observations has never, that we are aware, been made, nor has the amount of the persistent difference been determined. In the course of our investigations we have noted the amount and characteristics of the resting difference in the spinal cords of sixty-three Cats and fourteen Monkeys, and the results arranged in groups are given in Appendix B.

The most striking characteristics of the resting difference in the cord and the contrast between this difference and that of the nerve may be roughly seen after the death of the animal (Cat, Rabbit, &c.) by rapidly exposing a length of cord and of

the sciatic nerve, removing the exposed portion of each, placing it on a glass plate and bringing one electrode in connection with the cross section, the other with the longitudinal surface of the preparations. It will be found that in the Cat the nerve difference amounts to little over ·01 Daniell, whereas the cord difference amounts to ·025 to ·03 Daniell or more. That this contrast is not merely a question of cross sectional area is shown by experimenting with the dorsal cord of a small (young) animal and with the large nerve of a full grown adult animal of the same species, when the same relations will be found to still hold good, viz., the cord difference twice to three times the amount of that of the nerve.

For purposes of experimental investigation however, the spinal cord was exposed in the lower dorsal or lumbar region under all the precautions mentioned in the paragraph upon operative procedure; it was then divided and freed as required on either the central or peripheral side of the division for 4 or 5 centims. from all its attachments, the severed end was ligatured and this portion of cord raised from the canal and suspended in air by a ligature, still retaining its continuity with the exposed cord at its deep attachment. The raised portion was in some cases that on the central side of the section, in which case the continuity with the brain was preserved, in others that on the peripheral side, in which case the connection with the sciatic nerves was preserved.

1.—*Amount of Difference.*

(*a.*) *Whole Cord.*—If an average of the various results obtained in the case of fifty Cats is taken, the exposed cord being normal and always in connection by its deep attachment with a portion of cord *in situ*, but without distinction of the nature of this attachment, it will be found that the average resting difference in the Cat is ·032 Daniell, the highest difference being ·046 Daniell, the lowest ·014 Daniell.

A similar average of the results in nine Monkeys gives a resting difference of ·022 Daniell, the highest difference observed being ·029, the lowest ·013.

It is thus evident that the relationship between the amounts of the resting difference obtainable in the Cat and Monkey holds good for both the sciatic nerve and the cord, the amount in the Cat being very appreciably larger than that in the Monkey. The notable increase in the size of the resting current in the cord as compared with the nerve of the same species will be rendered evident if we place side by side the average results of the two. Thus :—

$$\frac{\text{Cat cord}}{\text{Cat nerve}} = \frac{\cdot 032}{\cdot 0095} = \frac{3 \cdot 3}{1}.$$

$$\frac{\text{Monkey cord}}{\text{Monkey nerve}} = \frac{\cdot 022}{\cdot 005} = \frac{4 \cdot 4}{1}.$$

That this increase in the proportion of about 4 to 1 is not merely due to increased

size has been roughly indicated previously; this will, however, be more clearly exhibited by the consideration of the ratio which a similar comparison between the difference in the cord and in the posterior root of the Cat shows :—

$$\frac{\text{Average Cat cord}}{\text{Average Cat posterior root}} = \frac{\cdot 032}{\cdot 022} = \frac{1 \cdot 5}{1}.$$

It is probable therefore that the larger difference is in some way correlated with the structure of the cord and the trophic and other physiological influences which that structure implies.

This explanation is supported by an analysis of the results obtained in the two species of animals when the cord is placed under different conditions as regards its central connections. Such analysis involves the grouping together on the one hand of all those determinations in which the cord was still in connection with the cerebrum and its central end investigated, and on the other hand of all those in which the portion of cord examined was that of the lower fragment unconnected with the cerebrum.

The first group shown in Appendix B, III., gives the average result in the case of the lower dorsal cord of fourteen Cats, this average being ·034 Daniell; the highest amount observed being ·046, the lowest ·025.

It also gives the average result in the case of five Monkeys, this being ·025 Daniell; the highest reading being ·029, the lowest ·018.

If now, we turn to the second group, the average in the Cat of all the readings in the dorsal and lumbar regions respectively when the Cat's cord is severed from the brain, amounts to :—

Dorsal region, 24 cases, average ·029
Lumbar ,, 10 ,, ,, ·033

34 cases

Gross average = ·03 Daniell.

Highest = ·043; lowest = ·014.

In the Monkey a similar average of four sets of experiments gives ·019 Daniell; highest ·027, lowest ·013.

A comparison of the two groups of results may now be made as follows :—

Cat—
- Cord connected with brain . . . . . ·034
- Cord severed from brain . . . . . ·03

Monkey—
- Cord connected with brain . . . . . ·025
- Cord severed from brain . . . . . ·019

The comparison shows that the amount of the resting difference in the anæsthetised animal is larger when the cerebral connections are intact.

This conclusion is supported by direct experimentation upon the influence of severance. Thus in an anæsthetised animal (Cat) the cord was exposed and divided at the level of the 4th lumbar vertebra and the central end ligatured. It was then suspended in the usual way and the electrodes attached to the cross section and the longitudinal surface. The resting difference amounted to ·044 Daniell, whereas, when the cord was severed higher up at the 7th dorsal vertebra, a notable fall to ·037 Daniell occurred.

In another experiment (Cat, 315) the cord was divided at the 13th dorsal vertebra and similarly prepared. Its central end was then connected with the galvanometer electrodes as above. The amount of the difference between the surface on the central side of the cross section and the cross section itself amounted to ·04 Daniell. A hemisection of the cord at the 8th dorsal vertebra was now made and the difference fell rapidly to ·38 Daniell, the rapid fall then ceased, but a slow fall continued for some time.

These experiments suggest that severance in an anæsthetised animal of the cord from the brain causes a direct diminution in the amount of the resting difference below the point of severance, whether by the interference with the circulation which such severance may imply, or by this aided by the interruption in the path which joins at any rate some of the (pyramidal) fibres with the cells with which they are in direct connection and which govern their nutrition. As will be seen later there is no evidence of a similar diminution being produced when the cross sections are made upon a portion of cord already severed from the brain by an interruption higher up. Hence the inference that the fall is correlated with the interruption (in the pyramidal fibres ?) is strengthened.

Finally the region of cord investigated has some relation with the amount of the resting difference. This is shown in Appendix B, III., in which observations made in the dorsal region are separated from those in the lumbar region.

The average of the dorsal region = ·029 ; highest ·043, lowest ·014.

The average of the lumbar region = ·033 ; highest ·04, lowest ·028.

Although the average seems to show that the difference in the dorsal cord is less than that in the lumbar, yet an examination of the highest and lowest limits suggests that the preponderance, in the latter case, is due to the fact that in the dorsal cord several very low readings were obtained. (See Table (2) ; Appendix B, III., Cats 194, 289, 349.)

We have endeavoured to get some notion of the relations of the different regions by exposing in an anæsthetised animal (Cat 36) the whole cord. This was then divided into three equal lengths, comprising the cervical, dorsal, and lumbar regions respectively, and the three placed in a warm moist chamber for examination.

The examination was made as rapidly as possible in the order given below, and at the various regions indicated.

Lumbar segment—			
From 4th lumbar	·035	to about 11th dorsal	·04.
Dorsal segment—			
From about 11th dorsal	·043	to about 3rd dorsal	·037.
Cervical segment—			
From about 3rd dorsal	·035	to about 3rd cervical	·037.

After a quarter of an hour's interval, the experiment was repeated in the reverse order, commencing with the cervical and ending with the lumbar segment. The results were as follows :—

Lumbar segment	·035	·036,
Dorsal segment	·030	·021,
Cervical segment	·031	·029.

In this experiment, the dorsal cord resting difference is greater than that obtained from either enlargement, but it is more affected by the injurious influences of severance and loss of circulation. It must be remembered, that there are three possible factors in the severed cord which determine the amount of the resting difference in any given region ; the number of fibres, the amount of grey matter, and the maintenance of vitality through circulation, &c., this last being influenced by size of vessels, &c. All these vary in different regions, but the first is preponderant in the dorsal region, the others in the enlargements.

(*b.*) *Cord Divided Longitudinally.*—In the course of experiments to be detailed hereafter, we had occasion several times to divide the cord longitudinally into two halves. This division was carried out under all the precautions indicated in the section dealing with operative procedure, and was always in the form of a longitudinal cut connecting the anterior and posterior fissures, and extended from the cross section of the divided cord for three centimetres. Since it was our main object to establish a quantitative comparison between the crossed and the direct excitatory cord effect evoked by cortical stimulation, the cord was generally divided in the lower dorsal region, and the lower end of the fragment on the central side of the division was split in the fashion just described. (See Plates 31, 33.) The results in seven Cats and five Monkeys are given in Appendix B, III.

Each half of the split cord was connected with a pair of non-polarisable electrodes by the cable arrangement already indicated, and the amount of the difference between the cross section and the surface in each then determined. It will be seen that the average amount for each side in the Cat is ·02 Daniell, the highest and lowest readings

being ·029 and ·01 in the case of the left side, and ·027 and ·014 in that of the right side.

In the Monkey, the average result for the left side is ·016, that for the right ·011. It will be noticed that in each animal the sum of the two readings is slightly larger than the average for the unsplit cord.

A further table (4) give the results of a similar splitting operation carried out on the upper end of the lower peripheral fragment of the divided cord in two Cats.

In one Cat (137) the left half of the split cord showed a resting difference of ·007, and the right ·016; in the other Cat (143) the left half showed ·021, and the right ·013. The amounts are considerably below those just mentioned, one reason doubtless being the fact that the portion of cord upon which the operation was carried out was severed from the brain.

(*c.*) *Cord previously operated upon.*—It has already been pointed out that, while severance from the brain seems to induce a condition in the separated cord in which the amount of the resting difference is less than it otherwise would have been, further operations upon this severed fragment do not seem to notably affect the difference, provided they are made in such situations as to leave a part of the cord both intact and *in situ* between their seat and the portion observed.

That is to say, the difference in the lower fragment of a cord severed from the brain is not further diminished by exposing it again in its continuity and performing there either section of one or of several columns.

It is different, however, when such operative lesions have been performed several weeks before the experimental investigation. In these cases the average amount of the resting difference observed was ·022 Daniell, that is less than the normal, but the differences between the experiments are best shown by reference to the column in Appendix B., III. (5). They will then be found to vary between ·012 (cord one month after section of posterior roots), and ·038 (cord four months after hemisection on left side). This last is an exceptionally high result when compared with that obtained after a very similar two months' previous hemisection when the amount of the difference was only ·017, and also that obtained after a one month's previous hemisection on the opposite side, when the amount was ·018.

In a case of one month's previous lesion of both posterior columns, the amount of the resting difference was found to be ·022, and after a lesion of one posterior column it was found to be ·025.

If ·030 is taken as the average amount of the difference in the normal Cat, after severance of the cord from the brain, then a descending series occurs in these cases, as shown in the table, in all of which with one exception the demarcation current is below the normal, and the average of these, when this exceptionally high and contradictory result is excluded, would be ·019 Daniell.

TABLE of Results after Previous Operations.

	·012	after section of posterior roots.
	·017	„ hemisection.
	·018	„ „
	·022	„ section of both posterior columns.
	·025	„ „ one „ „
Total ..	·094	
Average..	·019	Daniell approx.

2. *Alterations in Resting Difference.*

The electrical difference between the surface and cross section of the spinal cord alters during observation in the manner already described in treating of the sciatic nerve and root, but the alterations are much more marked.

(*a.*) *Physical Changes.*—The effect of drying is the same as in the case of the nerve, the amount of the resting difference continuing to rise steadily after exposure and isolation of the cord unless great care is taken to keep it moist. It is difficult to ascertain with precision to what degree this physical change is capable of causing a rise in the difference, this rise being about ·0001 Daniell in five minutes; but that it is by no means the sole agent is shown by the fact that even when the exposed cord is kept moist by steaming sponges with as much care as possible, the rise continues, though more slowly than when no such precautions are used, as also by the facts to be referred to in the succeeding paragraphs. It is, however, important to keep in view in the consideration of alterations supposed to be due to strictly physiological agencies the influence of these purely physical ones.

(*b.*) *Physiological Changes not obviously Excitatory.*—The alterations due to physiological changes are associated with both a rise and a fall in the amount of difference, and are much more marked in the case of the cord than in that of the nerve or the root. The amount of the rise is demonstrated in the following observations, in all of which the cord having been exposed, ligatured, and divided, was suspended by its unattached end and connected with the electrodes in the manner described before.

It was then observed that in every case the resting difference between the surface and cross section increased rapidly for the first five minutes or more after the isolation had been made, provided that the cord was still in connection by its deep attachment with a part which, being *in situ*, was in its normal physiological state of nutrition. The amount of this initial rise varies considerably in different cords, but the average in 19 cases amounted to ·0016 Daniell, the highest rise being ·003 and the lowest ·001. The duration of this comparatively rapid rise is, on the average, about five

minutes. This initial increase is probably of the same character as that observed by DU BOIS-REYMOND, HERMANN, ENGELMANN, and others in both muscle and nerve, and is in some way related to the development of changes produced by the cross section.

The difference continues very slowly to increase in the unstimulated cord, at a rate of about ·0001 in five minutes, this change being probably connected with interstitial drying. There is, however, a marked increase in the difference when the cord is aroused by successive stimulation, and this last rise is the most striking and novel feature displayed by the cord: it will be treated of under the excitatory changes.

If systemic death occurs, the difference immediately begins to decline, and this is such an invariable result that we have often observed the first approach of death by the behaviour of the galvanometer needle. On separation of the cord from the body a similar decline occurs, the rapidity of which is shown by the following results;—

DECLINE in Difference following Systemic Death.

		5 minutes.	10 minutes.	15 minutes.	20 minutes.	25 minutes.	30 minutes.
Cat (246) . . .	·029	·028	·026	·024	·023	·022	
Cat (258) . . .	·031	·03	·028	·026	·025	·024	·023
Cat (323) . . .	·039	·038	..	..	..	..	·03
Cat (345) . . .	·04	·037					

From the above cases it will be seen that on systemic death the resting difference declines to such an extent that in half an hour the total fall amounted to ·007, ·008, and ·009 Daniell. How far this fall is associated with the cessation of the circulation in the actual portion of exposed cord under investigation is a moot point, but the reasons brought forward on p. 283 with reference to the similar question in the case of the sciatic nerve are applicable to that of the spinal cord. The local circulation is undoubtedly seriously impaired by the exposure; it is, therefore, rather to the structural connection with the portion of cord *in situ*, in which the circulation is adequately maintained, than to the integrity of its own blood supply that the maintenance of the difference in the case of the living animal must be ascribed. It is wonderful what prolonged exposure a portion of the spinal cord will sustain without losing its excitability, provided only that the local conditions of adequate moisture and warmth are fulfilled and that a structural connection is kept up with normal unexposed cord substance.

The above decline is contemporaneous with a marked lessening of excitability. As is shown in the chapter upon cord excitation, all evidence of excitatory change in response to stimulation disappears a few minutes after systemic death.

If the fragment of exposed cord is wholly removed from the animal, the difference

rapidly subsides, as is shown in the experiment described on p. 313, as made upon such pieces of spinal cord.

The decline in the difference thus produced, seems to occur with greater rapidity than in the case of systemic death. It is illustrated by the following experiment upon the cord of the Cat (354), in which, at the close of an exposure and series of investigations, which had lasted an hour and a half, the exposed piece of cord was cut free from its deep attachments, and the consequent decline in the resting difference noted.

This difference had previously been rising all through the experiment, ever since the cord which had been exposed and divided at the 1st lumbar vertebra was first examined. The portion investigated galvanometrically was on the central side of the above section, but the upper part of the cord was not connected with the brain, since a second complete section at the level of the 7th dorsal vertebra had been made for purposes of stimulation.

The amount of the initial resting difference between the cross-section and surface of the investigated portion observed (at 11.4) was ·033 Daniell; at the close of the experiments (12.39) it was ·038; the exposed portion of cord was then severed from its deep attachment so as to be wholly detached; in two minutes (12.39) it was ·037;

(12.41)	. . . .	·036
(12.43)	. . . .	·034
(12.45)	. . . .	·033
(12.47)	. . . .	·032

That is to say, a fall in the difference amounting to ·006 occurred in ten minutes; in another hour the difference had fallen to half its original amount = ·019 Daniell.

Both the slower fall in consequence of systemic death and the more rapid fall in consequence of a complete detachment from the rest of the nervous system, contrast with that produced by the change following injury sustained by the cord even when *in situ*. The mechanical injury which seems most fatal to excitability, is that produced by stretching of the cord, a sudden pull being followed almost immediately by the disappearance of any excitatory effect and by a rapid fall in the resting difference Thus, in one animal (Cat 126), the difference was ·035, but owing to the arrangement for fixing the spine, &c., becoming loose, the suspended cord was pulled by a movement of the preparation, and the difference fell suddenly to ·017. The whole cord, however, was not injured, but only the portion observed, for a new dissection exposed a fresh part and a higher section was then made, which gave a difference of ·028.

(*c.*) *Physiological Changes connected with Excitation.*—It has been already indicated that a characteristic feature of the spinal cord difference is the alteration produced in it by stimulation. It will be seen by the experimental details, which are set forth in the following chapters, that marked excitatory electrical effects are evoked

in the cord by stimulating either the cortex of the brain, the different regions of the cord itself, or the issuing posterior roots. These effects resemble in character those evoked in the nerve trunks themselves; the electrical change commences with the stimulation, is opposed in direction to the resting difference, and subsides on the cessation of the stimulus. Following this true excitatory effect is an after-effect, which is characterised by an increase in the previous difference.

In any given experiment the after-effect shows itself thus. The cord having been exposed, divided, prepared, and connected in the usual way with the electrodes by its cross section and its longitudinal surface, the amount of the resting difference was noted. This difference rises as just stated for the first few minutes, and then remains very nearly steady. The cord is now excited in any of the three ways mentioned above; an electrical change occurs, *i.e.*, a current opposed to the difference is present in the galvanometer circuit which, on the cessation of the stimulation, subsides. The galvanometer needle, which evidences the existence of this current, having moved from its resting zero position through a certain deflection, returns to its previous position. If the nerve were the tissue under investigation, this return would be not quite complete, but with the spinal cord it is characterised by continuing beyond the zero position to a point considerably the other side, after which the needle slowly moves back again towards zero, which, however, it does not reach. As the result of excitation, therefore, the previously balanced difference is no longer compensated; a current persists in the circuit in the direction of that produced by the difference, and to compensate this, and thus bring the needle back to zero, the balancing circuit has to be readjusted.

In short, the excitation has caused, after the usual negative variation, a permanent rise in the resting difference between the two electrode contacts. This, positive after effect is not unknown in other structures, it occurs occasionally in both muscle and nerve preparations of the Frog (Hering, Head), but the conditions necessary for its production are but imperfectly ascertained. It is, however, as far as we know, invariably present in the case of the spinal cord of the Cat and Monkey, though its amount is very variable in different preparations.

In almost all cases the amount of the rise is dependent rather upon the condition of the preparation than either the intensity or duration of the cord stimulation. It is greatest as a consequence of the earlier stimulations, and becomes less and less with a repetition of the stimulus.

If, therefore, a series of experiments are made involving the stimulation of the cord at successive intervals, the resting difference rises at first rapidly, and then more slowly, until after 20 to 30 stimulations in from 30 to 45 minutes, the rise finally practically ceases.

The stimulus used, whether applied to the cord or to structures connected with the cord, was in all cases that of the alternating induced current previously alluded to in the chapter on the experimental method. The amount of the total rise observed in

different cases varied according to the seat of the stimulus which evoked the cord change. This seat may be either (A) *Brain*, (B) *Nerve*, or (C) *Cord*, and the cases in which we specially noted this change are as follows :—

A. Cortical Excitation. Cord connected with Cortex.

	Initial difference.	Final difference.	Total rise.
Cat (114)	·037	·039	·002
„ (124)	·046	·047	·003
„ (126)	·036	·040	·004
„ (308)	·033	·036	·003
„ (319)	·030	·035	·005
„ (323)	·032	·033	·001
Monkey (234) . .	·026	·029	·003
		Average rise	·003

B. Nerve Excitation (sciatic). Cord severed from Cortex.

	Initial difference.	Final difference.	Total rise.
Cat (121)	·031	·034	·003
„ (143)	·032	·035	·003
„ (145)	·028	·035	·007
„ (148)	·023	·026	·003
„ (153)	·025	·029	·004
„ (192)	·023	·030	·007
„ (194)	·017	·020	·003
„ (327)	·023	·034	·011
„ (339)	·022	·030	·008
„ (344)	·022	·025	·003
„ (170)	·026	·029	·003
		Average rise	·005

C. Cord Excitation. Cord severed from Cortex.

	Initial difference.	Final difference.	Total rise.
Cat (196)	·017	·030	·013
„ (244)	·027	·029	·002
„ (245)	·021	·026	·005
„ (357)	·032	·038	·006
„ (366)	·030	·037	·007
„ (355)	·037	·041	·004
„ (371)	·028	·035	·007
„ (375)	·032	·045	·013
„ (378)	·027	·029	·002
„ (243)	·027	·029	·001
„ (354)	·033	·038	·005
		Average rise	·006

These results indicate (1) that the rise in the difference is occasioned not merely by the direct application of the stimulating agent to the cord, but as a consequence of the presence of a series of excitatory processes, whether these are produced by nerve impulses entering below by afferent channels, or from above by cortical efferent ones. This conclusion is supported by the fact that a similar rise follows a large reflex discharge of energy from the cord, when this is produced in the strychnised animal by sensory stimulation.

(2.) They also show that the rise is least in the case of the excitatory cord changes evoked by cortical stimulation, in which case the limit of rise is not only small, but soon attained, the average rise in the instances given under A being ·003, the maximum = ·005, the minimum = ·001. When the sciatic nerve or posterior root of the cord (severed from the brain) is excited, the rise is seen to be much more pronounced, being on the average ·005, maximum ·011, minimum ·003. Finally, when the columns of the cord itself are excited, the rise is greater, the average being ·006, maximum ·013, minimum ·002. (The average rise in this case would be still greater if the three very low and exceptional readings of ·002 were omitted from the table; it would then be ·0075.) In the same experiment performed on the Monkey (232) the rise in half an hour following twelve excitations was ·006.

It would thus appear that one of the main features in the rise is the extent to which the nerve structures in the cord are thrown into activity; the result of cortical excitation is to awaken impulses in a more limited area of the cord than is the case with excitation of the sciatic afferent nerve fibres, and this latter does not cause such a widespread awakening as is produced by direct cord stimulation.

From these results alone no conclusions of a definite kind can be drawn as to the relations subsisting between the cord and the brain on the one hand, and the cord and the nerves on the other, but if the amount of resting difference may be truly

taken to be an indication of the amount of potential energy, which the nerve material is capable of making kinetic in the form of a nerve impulse, then this remarkable rise, and the conditions which determine it, would appear to show that the physiological characters of the structure upon which the storage of energy depends, are such as to be rendered more efficacious with use, and that the central structures (cells) of the cord play the most prominent part in this influence of functional use upon efficiency.

CHAPTER V.—ON THE ELECTRICAL EFFECTS EVOKED IN THE SPINAL CORD AND MIXED NERVES BY EXCITATION OF THE CORTEX CEREBRI.

The primary object of this work being the determination of the nature of the impulses which issue from the excitable or so-called motor cortex, considerable importance attaches to positive results on this point. As, however, usually happens in the employment of a new method, we have found that more actual advance was made by applying it to the study of the lower centres and fibres through which these impulses pass than by attempting to elucidate the functional relations existing between one part of the cortex and the rest of the encephalon.

One fundamental fact stands out, however, prominently, viz., that, as we shall see directly, it is possible to ascertain and judge the nature and comparative amount of the electrical changes which accompany the descent of the cortical impulses in the spinal cord, and so to learn the character of the cortical discharge. Practically, therefore, the results of our special investigation of the excited cortex will best be arranged according to the part of the nervous system in which the electrical changes were observed. A further subdivision of such a classification will be necessary in order to bring out the wider points of interest which have received elucidation by the use of this method, and this is furnished by the summary and arrangement we have given on pp. 272–276, of the facts discovered by other methods, of which the most notable are those of simple inspection and of graphic record respectively.

In accordance with this plan, therefore, we will commence with considering the case in which we observed the electrical changes in the dorsal cord, with the object of ascertaining the character of the descending nervous impulses in consequence of stimulation of the cortex.

We have employed in these experiments on the relations of the cortex cerebri to the bulbo-spinal and peripheral systems fifteen Monkeys and thirty-two Cats.

Excitation of Cortex.

1. *Electrical Changes Observed in the Spinal Cord.*

The arrangement expressed in the above headings is the fundamental experiment designed to elucidate, if possible, the nature of the impulses which pass from the cortex to gain and traverse the bulbo-spinal centres. The desirability of avoiding shock, which so markedly lowers the excitability of the cortex, led us to choose to investigate the electrical effects which accompany the impulses as they pass through the mid dorsal region, so that the section of the cord was made in the Cat immediately below this point, and in the Monkey, just above or through the uppermost part of the lumbar enlargement. (See figs. 4 and 5.)

This selection of the seat of section had the additional advantage that it enabled us to proceed at once to the determination of further points, viz., the localisation of the upper and lower limb areas in the cortex, and thus to generally control the results obtained, as will be shown presently. We will first describe a typical experiment.

The anæsthetised animal having been arranged as described (Chapter III.) the dura mater was exposed over the so-called motor area of the lower limb; the spinal cord was then exposed at the level of about the 7th dorsal vertebra, raised in air and connected to the non-polarisable electrodes. The character of the resting electrical difference between the cut end of the cord and the uninjured surfaces of the columns was noted as set forth in Chapter IV.

(*a.*) *Effects seen in the Electrometer.*

The electrodes were, in the first instance, connected with the capillary electrometer.

The dura mater was then opened, and the surface of the cortex excited (*vide* p. 299). The effects observed in the electrometer were—

(1.) A persistent negative variation of the difference lasting as long as the excitation was applied to the cortex.

(2.) A series of intermittent negative variations commencing (sometimes after a short interval had elapsed) from the cessation of the excitation, and continuing for a variable period according to the state of the cortex.

We may with advantage at once briefly review the general questions raised by this result, as such a discussion will make clearer the object of further researches.

The effect seen in the electrometer was so identical in character with that obtained from the muscles in an epileptiform convulsion started by similar excitation of the cortex as to suggest that the essential features of the muscular convulsion are wholly due to the character of the cortical discharge. This is illustrated by the

Fig. 4.*

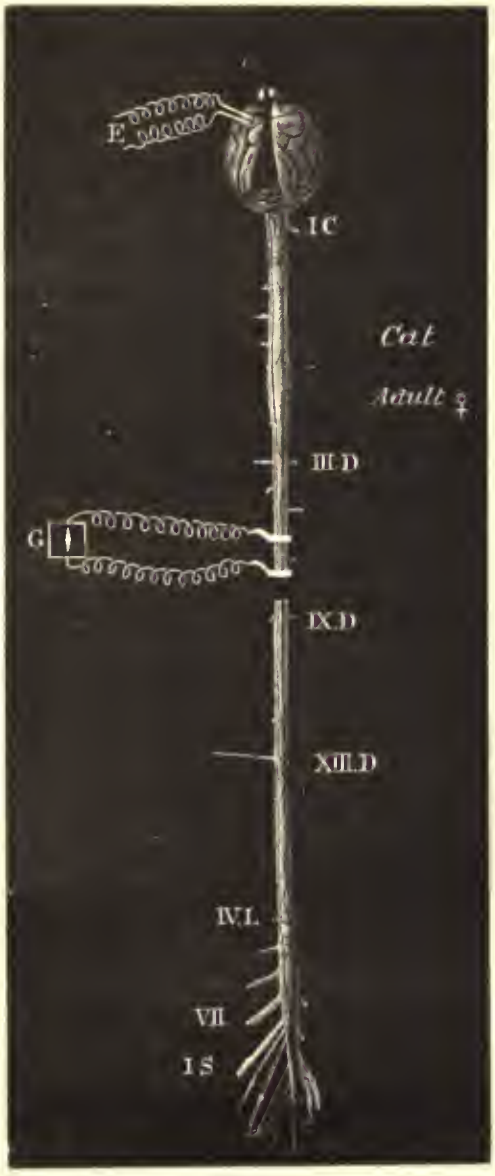


Fig. 5.

* The central nervous system displayed in this and succeeding figures is a photographic reduction of a full size photograph of an actual dissection, as shown also in Plates 30–33. By this means, exact topography of all experimental details (*i.e* position of electrodes, &c.) has been preserved. It is, perhaps, hardly necessary to add that the amount of cord exposed is shewn in Plate 29.

annexed woodcut (fig. 6), in which two records, one of the muscle, the other of the movement of the electrometer, are contrasted. The lower tracing, G, is that of the muscular movements of the rectus femoris of the Cat; the upper, E, is that of the movements of the projected image of the mercurial meniscus of the electrometer photographed on a sensitive plate. The juxtaposition of the records was effected by a photographic reduction of the two tracings. It is necessary to point out that exact comparison is not possible, since the two records were obtained from different animals; they are, however, comparable in this sense, that since we have selected in each case fits of about the same degree of intensity, the general fused character of the first stage, and the interrupted character of the second stage, is similar in each.

Further, the change in character of the interrupted stage itself as the fit draws to its close is very noticeable, the great increase in the extent of each clonic spasm accompanying the slower rhythm is, as will be seen, a feature common to both records.

It will now be advisable to consider in more detail the character of these electrical variations.

A reference to the photograph of the movements of the electrometer, in fig. 6, will show that the first stage of the effect produced in the cord by exciting the cortex, *i.e.*, the tonic variation lasting during the period of excitation, is a complete fusion of impulses, so that it is with our present instruments impossible to detect any waves or intermissions in it. In this respect the tonic stage exhibits no

Fig. 6.

E. Photograph of movements of electrometer.
G. Tracing of contracting muscle.
t. Tracing of time signal with intervals of $\frac{1}{10}$th sec.

difference from the tonus obtained by exciting the corona radiata after the cortex is removed. It is otherwise with the graphic method, see p. 273, in which a rhythm or period can be seen, showing the tonus to be an imperfect fusion of contractions. Until the question is re-examined with still more delicate instruments, it must be left entirely open, as the absence of intermittence in the electrical record may be due to instrumental inadequacy. We cannot, however, refrain from suggesting that it may be possibly a genuine phenomenon, and that the waves seen often on the tetanus curve, in the graphic method, may be in relation with blocks in the motor path; one such block we have found to be offered

by the bulbo-spinal centres to the passage of the impulses, from the spinal cord out into the nerve (see p. 458, Chapter X.). The further recent experiments of WEDENSKII* seem to suggest that these waves in the muscular record may be to some extent in relation with the block offered by the motor endings of the nerves in the muscles, since he finds that such muscular intermittence may be produced by stimulation of the nerve itself with rapid rates, an intermittence which, not being synchronous with the rate of stimulation, but having its own rhythm, is presumably referable to the neuro-muscular mechanism.

As regards the after effect, the clonic stage, it is frequently separated from the tonic stage by a distinct pause or interval; this is of course visible in all methods of exploration, to which the electrical investigation of the spinal cord is no exception. When it occurs, therefore, it is obvious that after the cortex has been roused to discharge, thus evoking the tonic stage, it possesses the power of again emitting impulses when thrown into a high state of excitation. The period at which this clonic discharge commences is variable, there being in some instances a pause or period of delay, whilst in others the intermittent or clonic stage may even overlap the tonic condition, which, consequently, ceases prematurely, while yet the excitation is being continued.

The clonic stage, or after effect, has a distinct rhythm (see graphic method, p. 273), in which the muscles respond to intermittent impulses. Exactly the same is seen in the electrical changes of the spinal cord. This stage, or after effect, as it truly is, presents three chief features for study:—(1) Its commencement; (2) its development; (3) its mode of termination; these being common to both the muscular and the spinal records.

(1.) The clonic stage invariably begins with small, often single discharges, *vide* fig. 6, these soon increase in strength. This is of course closely imitated by the graphic records of the muscle, the contractions of which, minimal at first, become, later, maximal.

(2.) The further development of the stage is marked by summation of the impulses, the rhythm of which, directly measured, appears to be about 10 per sec., but we have not yet had time to thoroughly investigate this point. (*Vide* graphic method, p. 273.)

The summation of the electrical variations very obviously harmonises with all the other facts relating to the persistence of the muscular contraction, when produced by cortical stimulation. (See also FRANÇOIS FRANCK and BUBNOFF and HEIDENHAIN, *loc. cit.*)

(3.) The termination of the series of intermittent variations is marked by their becoming fewer, larger, and finally ceasing abruptly (*vide* fig. 6), very rarely diminishing to final disappearance.

* WEDENSKII, 'Archives de Physiologie Normale et Pathol.' (BROWN-SÉQUARD), Jan., 1891.

The absolute values obtained in the electrometer varied in the two stages, as estimated by the eye, and the rough estimate thus formed is supported by the better evidence of the photographs. They average 2 divisions, rarely 3 divisions for the tonic stage, and 1·5 divisions for the clonic stage.

It would appear that this is true for the Carnivorous animal, as represented by the Cat (eleven animals observed). Whether these electrometer figures are the same for the Monkey we are unable to say, as we devoted our attention in the experiments on that higher Mammal (seven animals observed) to photographing the results.

The absolute electromotive values obtained by the electrometer and recorded photographically, are being examined by Mr. G. F. Burch at the present time, and we, therefore, will postpone the further consideration of this most important point.

(*b.*) *Effects seen in the Galvanometer.*

The total effect produced in the galvanometer when it is connected with the spinal cord, and the cortex is excited, resembles the records of the muscular contractions, in that there are two distinct stages. It need, however, hardly be said that the slow swing of the galvanometer needle is incapable of recording intermittently, and consequently both stages are composed of a series of summated effects. The rate of movement of the needle is notably different in the two stages, and the close observation of this feature proved of much value in other experiments, notably those on the corona radiata, see p. 337.

In the first stage the needle generally begins to move soon after the commencement of the cortical excitation (see Method, p. 299), but often owing to one of the depressing circumstances mentioned on p. 272, the cortex is not normally excitable and the effect it produces when stimulated is consequently delayed. The needle swings steadily during the excitation, but when this ceases there is a distinct check,* and then as the after-effect develops the needle slowly swings on and gradually comes to a standstill at the end of the second stage or after effect. The mode of termination of this last is slow and deliberate in its gradual diminution, thus contrasting markedly with the abrupt cessation of the galvanometer excursion, when the corona radiata or spinal cord is excited. This gradual dying out of the effect is so absolutely characteristic of the cortex that it can be used for differentiation.

Though well aware of the small value to be attached to the quantitative use of the galvanometric readings thus obtained, we venture to add a few remarks on these in view of the novelty of the point.

When the central end of the whole cord is connected with the galvanometer, and

* What is said on p. 299, &c., relating to possible errors and fallacies may be here remembered as showing that this check is purely a physiological phenomenon, there being no possibility of the excitation current affecting the delicate galvanometer.

one cortex (*i.e.*, lower limb focus) excited for a definite period, an electrical excitatory variation is produced in the cord, the amount of which is indicated by the following average of several observations.

	Duration of excitation.	Average strength of excitation.	Average variation.
Cat	5 seconds	8500	193°
Monkey	3·5 „	4500	175°

The brain of the Monkey was stimulated for a shorter time, and with far weaker excitation than that used for the Cat, in consequence of our desire not to make the cortex hyperexcitable. Even then the excitatory effect in the Monkey is nearly as large as that in the Cat. The truth of this position is also evidenced by numerous observations we have made under other circumstances, the Cat always requiring a stimulus, which in the Monkey would have evoked a far higher excitatory effect. As with all results obtained by the method of averages, no doubt this point would repay accumulation of observations, since, although no absolute value can be given to the figures, they seem to show specific differences. With the cord divided longitudinally, and the excitatory effect observed in each half, this absolute difference apparently disappears (see p. 354).

Before proceeding further, it is essential that we should indicate the experimental evidence on which we base our interpretation of the electrical changes in the cord.

That the changes are due to the discharge of excitatory impulses from the cortex is clear, but it may be asked what evidence apart from the parallelism discussed on p. 324 there is to show that they are the concomitants of the passage of actual nerve impulses through the portion of exposed cord, and not the results of conduction from the electrical changes evoked in all the surrounding muscles which are thrown into spasm.

The evidence which shows that the change is one localised in the nerve fibres of the exposed cord may be grouped as follows :—

(1.) The position of the electrodes being arranged to ensure isolation, as described in Chapter III., p. 295, this isolation is sufficiently complete to allow of the surrounding muscles being thrown into activity without any electrical change in the exposed tract being evident in the galvanometer.

(2.) In observations made in the Monkey with the freshly exposed cortex, the initial and immediately succeeding stimulations of the lower limb area evoked effects which, with the strength of the stimulus employed, were so exactly circumscribed that, since the cord was divided and the lower limbs thus cut off, no demonstrable

muscular movement of any kind existed, yet a marked and distinct electrical change of the usual kind was present in the cord and evidenced both in the electrometer and the galvanometer.

When, further, owing to prolonged excitation, exposure, or slighter degree of etherisation, hyperexcitability of the cortex became established, subsequent excitation evoked a more general discharge, and although the muscles of the trunk and upper limb were now thrown into active contraction, the change evidenced by the electrometer and galvanometer remained similar in character to that previously observed.

(3.) If in any given instance with the central end of the spinal cord in the lower dorsal region exposed and connected with the galvanometer electrodes, the cortical area for the upper limb was excited, no effect was observed in the galvanometer and electrometer, although the muscles of the upper limb were thrown into convulsion.

(4.) The injury (cutting off, &c.) of the cord between the exposed region and its deep connections abolishes the effect in the cord, even although the muscles are thrown by cortical excitation into violent spasm.

(5.) In addition to the above, the whole mass of results to be detailed in this and the succeeding chapters is convincing evidence of the truth of our interpretation, since, as will be seen by separating the fibres in the two sides of the cord (longitudinal section), by interrupting the fibres on one side only (hemisection), &c., we obtained a differentiation in our results which admits of no other explanation than the one upon which we base our deductions, namely, that the electrical effects observed are due to changes localised in the exposed cord, and, moreover, in the experiments under discussion localised particularly in the nerve fibres which form the pyramidal tracts.

The fact above alluded to of the absence of electrical effects in the dorsal cord when the area for the upper limb was excited in the Monkey, involves matters of such importance that we now pass on to consider it in some detail.

(*c.*) *The Localisation of Efferent Representation in the Cortex as ascertained by the Electrical Method.*

It was clear from the commencement of this research, that our method afforded means of differentiating the centres in the cortex and their correlated fibres in the spinal cord. We accordingly made observations of the following character:—

Having exposed the cortex freely, and connected, as before, the cut dorsal cord with the electrometer, we proceeded to obtain the usual result by exciting the lower limb area with a minimal but adequate stimulus, evoking thus an effect without at the same time developing an epileptic hyperexcitability of the cortex. We then explored the rest of the surface of the so-called motor region with the electrodes and the same strength of excitation, to see how far we could determine whether there was

any electrical change in the cord, *i.e.*, the pyramidal tract, really belonging to the lower limb, when other parts of the cortex were excited. As will be now shown, our instrument gave no indications of such diffused effects, but in this relation we must draw attention to the animals used (Cat and Monkey).

Considering that the minute differentiation of efferent motor function in the cortex of the Cat is relatively insignificant compared to that in the Monkey, we employed the former animal for the preliminary investigation of the accuracy of the general position which is involved in our first statements. But we also found in the Cat that, while with a given strength of excitation, stimulation of the lower limb cortical area gave the definite result of a movement of two divisions in the electrometer (the connection of the cord, &c., being as stated before), the excitation of the occipital lobe and the temporo-sphenoidal lobe respectively gave no result at all. Upon this point it may be remarked that in some instances we were able in the Cat even to differentiate, as we easily could do in the Monkey, between the upper limb and the lower limb areas. That is to say, that if the dorsal cord were observed, we got a well-marked effect by exciting the lower limb focus (as indicated by FERRIER), whereas excitation of the fore limb focus produced no visible change in the cord's state, as evidenced by the electrometer.

Thus the following facts were noted in the Cat (126).

CORD led off at Lower Dorsal Region.

Regions of cortex excited.	Strength of excitation.	Effect in Electrometer.	
		Tonic stage.	Clonic stage.
(*a*) Lower limb focus	10,000	Rise 2 divisions	1·5 divisions
(*b*) Occipital lobe	10,000	Nil	Nil
(*c*) Temporo-sphenoidal lobe .	10,000	Nil	Nil
(*d*) Fore limb focus	10,000	Nil	Nil

For the points *a*, *b*, *c*, *d* excited, see Plate 30.

Turning now to the Monkey, we carried this mode of investigation still further by the employment of minimal stimuli. The following general result was obtained. The dorsal cord being observed, the greatest effect was produced when the excitation was applied to the centre of the lower limb area, *i.e.*, just at the hallux focus,* and this effect diminished as the electrodes were removed from that point towards the mesial surface of the hemisphere or downwards over the convex surface towards the superior frontal sulcus. (See Plate 32.) It was interesting to observe that opposite this sulcus,

* BEEVOR and HORSLEY, 'Phil. Trans.,' 1890, &c.

where, according to BEEVOR and one of us, the upper and lower limb areas tend to overlap, with the same stimulus as in the latter case this region was the last from which any effect could be produced in the fibres of the dorsal cord. Even in the case where the whole cortex was very excitable, and where a generalised effect was thus easily evoked, and where, consequently, electrical effects in the cord followed stimulation of the upper third of the upper limb area, the general effect was, nevertheless, most markedly graduated from the centre of the lower limb area in diminishing order as the electrodes were removed downwards and passed the level of the superior frontal sulcus.

We may now allude to the obvious inference that might be drawn from these experiments, namely, that although there is no sharply marked line of demarcation between the cortical foci, there is nevertheless in the facts we have just stated a certain amount of evidence against the assumption that the lower limb, for example, is represented to any marked degree in the upper limb area of the cortex. We do not speak with great positiveness on this point, because it may well be that the instrument we chiefly used in this branch of our work, the electrometer, was not sufficiently delicate to show the extremely minute variation which might be supposed to result from the excitation of only a very few fibres. That this indeed seems probable is shown by the results of two experiments which we performed with the galvanometer instead of the electrometer. Unfortunately, however, they do not enable us to speak with greater certainty in the directions indicated, because in each instance the cortex was hyperexcitable from the commencement of the experiment. This, however, is clearly a branch of enquiry which might with advantage be followed out by subsequent observers.

In this connection the experiments of SHERRINGTON* are very suggestive, and we shall refer again to this part of the subject in describing our experiments on bilateral representation.

(*d.*) *The Amount of the Galvanometric Readings.*

Although, as has been stated, no exact comparison for quantitative purposes can be made between different deflections of the galvanometer, when, being connected with the central end of the exposed spinal cord, the cortex is excited, yet the amounts of the different readings are in themselves of great interest, owing to the fact that it is always possible with an excitable cortex and a sufficiently strong excitation to obtain very large galvanometric deflections. It is obvious that the deflection is dependent not merely upon the intensity but the duration of the stimulation, hence the excitation was limited by the revolving key, previously described, to 5 seconds. Since, however, the cortical discharge lasts a variable time after the stimulus has ceased,

* 'Proceedings of the Physiological Society,' 1890.

the galvanometric effects display, as might be expected, great inequalities; these, however, will be seen to be in strict relation with the amount of visible contraction evidenced in the muscles of the trunk, &c., and hence are really determined by the force and duration of the cortical discharge. Bearing this in mind, the following table is very instructive, as indicating the size of the deflections, which vary, as is seen, from 63 to 510 scale. The intensity of the stimulus, the particular cortex excited, and the character of the fit evoked, are in each case noted.

It will be seen that the average of these readings, which were all taken in four animals (Cat), as far as possible under similar conditions of etherisation, &c., amounts to 193 scale. It will be also seen that it is always easy to produce by a sufficient intensity of stimulation readings which are in excess of this.

GALVANOMETRIC Effects produced in Spinal Cord of Cat by Cortical Excitation.

	Intensity of Excitation.		Galvanometric Effect.	Muscular Movement.
Cat (315) . . .	8,000	5″ left cortex	63	Slight fit
	8,000	,, right ,,	115	,, ,,
	9,000	,, left ,,	108	,, ,,
	9,000	,, right ,,	230	Good fit
,, (317) . . .	8,000	,, left ,,	50	Very slight fit
	10,000	,, ,, ,,	162	Fair fit
	12,000	,, ,, ,,	235	Good fit
	8,000	,, right ,,	130	Slight fit
	10,000	,, ,, ,,	185	Fair fit
	12,000	,, ,, ,,	230	Good fit
,, (319) . . .	10,000	,, left ,,	90	Slight fit
	12,000	,, ,, ,,	170	Fair fit
	10,000	,, right ,,	150	,, ,,
	12,000	,, ,, ,,	260	Good fit
,, (324) . . .	6,000	,, left ,,	260	Slight fit
	8,000	,, ,, ,,	340	Fair fit
	10,000	,, ,, ,,	510	Powerful fit
			17 = 3288	
		Average. . . .	193	

The interest of the results will increase when we compare the average amount with the highest obtainable value of the galvanometric reading afforded by the effect of cortical excitation in the sciatic nerve. It must be now pointed out that in all cases, it is essential to reject observations in which there are sudden irregular changes in the resting electrical difference of the cord, since these are in great measure due to slight failure of the anæsthesia and to the consequent semi-voluntary discharge of cortical impulses.

(*e.*) *Electrical Change in Cord produced by "Semi-voluntary" Cortical Discharges.*

During prolonged etherisation it is well known that animals of all kinds, including Human beings, occasionally make unconscious, but semi-voluntary, purposive movements. These movements are abolished by very profound anæsthesia.

Electrical effects manifest themselves in the observed portion of exposed spinal cord when these semi-voluntary movements occur in the upper limb and trunk muscles. The effects are evidenced in the galvanometer connected with the tissue by deflections, which, though resembling the excitatory variations in being always opposed in sign to that of the resting difference, vary very much in amount and rapidity of development. It is obvious that the excitability of the cortex and the intensity of the exciting agency, must be the chief agents in determining the amount of this effect. The extent of such a deflection when, as evidenced by well-marked movements of the muscles on both sides in the upper half of the body, a considerable cortical discharge of energy was taking place, has amounted in the Monkey to 360 scale; it was however, at once abolished by profound anæsthetisation. As a rule the deflections amounted to from 20 to 60 scale; no doubt they would have been larger, had it not been for the fact that, since their appearance interfered with accurate observation of cortical effects evoked by stimulation, we always took care on perceiving them to so alter our conditions of anæsthesia as to abolish this source of error.

2. *Electrical Changes in the Sciatic Nerve.*

After having thus considered the electrical changes produced in the spinal cord by the functional activity of the cortex, we next turned our attention to the more complex question of what occurs in the peripheral nerves when the cortex is excited. This is obviously more complex, because, although we are still exciting the cortex, we have now introduced into the mechanism the bulbo-spinal system of centres, so that we are brought at once face to face with the question as to how far the changes which we have just been studying in the spinal cord are modified by the as yet hypothetical termination of the fibres of the pyramidal tract in the said bulbo-spinal centres.

We are justified in expressing this query in a still simpler fashion: what becomes of the cortical impulses when they reach the bulbo-spinal centres? Other things being equal, it might have been expected that we should have got very clear evidence of the effect of active excitatory change in the peripheral nerve, seeing that if this had been still in connection with the muscle, the muscle would have been thrown into a powerful series of contractions. It was, therefore, with very considerable surprise that we observed what a relatively small electrical variation was obtainable in the sciatic nerve when the corresponding portion of the cortex was excited. The experimental procedure was extremely simple, and as follows:—The cortex was exposed, as described, and the sciatic nerve on the opposite side of the body was also exposed,

ligatured, divided below the ligature, and its central end connected in the manner indicated in Chapter III. with the galvanometer or electrometer electrodes. (See fig. 7.)

Fig. 7.

We found that excitation of the cortex in most cases produced no perceptible effects when the capillary electrometer was in connection with the nerve, and when occasionally effects were seen, their complete absence in other instances, and their rapid disappearance on repetition, threw doubt on the observations.

With the galvanometer, however, effects could always be seen, though these were very small in amount as compared with those observed in the spinal cord. In a few cases, however, in which the excitation applied to the cortex was very intense, so

as to arouse very violent and prolonged bilateral fits, the deflections observed approached in size the smallest of those obtained in the cord. The general results will be seen by the following table, in which the effects observed in the nerve on the opposite (*i.e.*, corresponding) side to the excited cortex of eleven Cats and two Monkeys are separated from those observed in the nerve on the same side. The table is so arranged that the weak fits are given first and the stronger prolonged ones last.

It will be seen that the amount of deflection varies from a mere trace to 80, the larger readings being always obtained in the case of powerful prolonged and bilateral fits. The average of all the readings in the nerve opposite to the excited cortex is 31, whilst under no circumstances, even with the most powerful fits, is an effect obtained equal in amount to the change evoked in the spinal cord.

	Intensity of Excitation.	Duration of Excitation.	Effect in Nerve Opposite to Cortex.	Effect in Nerve on same Side as Cortex.	Character of Fit.
		Secs.			
Cat (291)	12,500	5	2	..	Weak
„ (293)	10,000	„	7	..	„
			6	..	„
„ (296)	11,000	„	5	..	„
			9	..	„
			12	..	Slight
			20	..	Fair
„ (299)	12,000	„	12	10	Weak
			20	..	Fair
			10	..	„
„ (290)	„	„	18	2	„
			10	..	„
			22	..	„
„ (71)	6,000	„	20	..	„
Monkey (54) . . .	5,000	$3\frac{1}{2}$	16	5	Good
			18	1	„
„ (217) . . .	„	„	28	18	„
			18	..	Moderate
			16	5	„
Cat (298)	12,500	„	28	..	Good
„ (75)	„	„	35	..	„
			28	..	„
	10,000	„	35	..	Violent
			55	..	Prolonged
„ (292)	12,500	„	62	..	Prolonged powerful fits
			46	..	
			80	..	
„ (79)	„	„	„	..	Prolonged powerful fits
			„	..	
„ (301)	12,000	„	70	80	Prolonged powerful fits (morphia)
			28=868		
		Average ..	31		

If we select out of the whole table those readings which were obtained with fits of a unilateral character, thus disregarding the whole of the larger numbers, we find that the average amounts to 20, this being very much below the average unilateral effect in the cord. (See Chapter VII.)

It might be imagined that this difference in amount between the nerve and cord effect was entirely connected with the difference in sectional area and thus in resistance; that this is not the case is shown by the following considerations :—

(*a.*) The total resistance in connection with the preparation is made up of the electrodes with their cables and the tract of tissues, of these the resistance of the cables is far in excess of that of the tissue, and hence any difference in resistance between the spinal cord and nerve preparations due to the sectional area of the tissue is but a small fraction of the whole.

(*b.*) The absence of effect in the capillary electrometer, when connected with the nerve, shows that any unusual resistance which may be offered by the nerve as compared with the cord is not the cause of the diminution, since the amount of the electrometer movement is unaffected by changes of resistance.

(*c.*) The sectional area of the nerve of an adult large Cat is nearly as great as that of the dorsal cord of a young animal or a small Monkey, yet the effect is small in the former and large in the latter structure.

(*d.*) As will be seen in Chapter VII., on bilaterality of representation, it is possible to obtain large effects in only one-half of the cord, split longitudinally. This portion has apparently less sectional area than the sciatic nerve, but the electrical change in it, as will be seen by reference to the tables, is far in excess of the nerve change.

(*e.*) The change in the cord is undoubtedly one connected with the fibres of the pyramidal tracts, it is therefore with reference to their sectional area as compared with the area of the motor nerves in the sciatic nerve that any criticism on this head should be directed. There is, however, every reason for supposing that the pyramidal tracts in the dorsal region are smaller in cross section than the sum of the anterior roots of the lumbar plexus.

These considerations serve to emphasize the conclusion to which, as it appears to us, the foregoing results tend, viz., that the extraordinary difference in quantity between the electrical effect in the cord and in the sciatic nerve when the cortex is excited, must be attributed to an alteration in the quality and quantity of the nerve impulses in their passage from the cord into the nerve, and that the structure of the spinal centres, through which the impulses must necessarily pass to reach the issuing nerves, so influences the transmission as to cause this striking change. This view is strengthened by the remarkable confirmation which is given to it by experiments in which both the spinal cord is directly excited and the centres in it discharged reflexly by stimulating its posterior roots. It will be seen (Chapter X., p. 478, and Chapter XI., p. 494) that under these circumstances the electrical effects produced in the sciatic nerve are extremely small and resemble in amount those above referred to.

The largest effects we have ever seen in the nerve in consequence of cortical excitation have been obtained by the use of absinthe. The powerful general fits which followed the introduction into the blood of this drug being evidenced in two animals (Cat) by effects which have amounted to 272 scale. It need hardly be pointed out that such fits are of extremely prolonged character, and that in the spinal cord electrical changes occur which give deflections in very many cases too large to be read (off screen).

Cortical Localisation as Evidenced by Electrical Changes in the Nerve.

The electrical changes in the nerve, as evidenced by the galvanometer, although small, are quite definite, and afford additional proof of the localisation of cerebral representation. Thus, when an adequate stimulus was employed, which was, however, only intense enough to evoke unilateral muscular contractions, the electrical change in the nerve was entirely confined to that on the opposite side to the excited cortex. This subject will be discussed in detail in Chapter VII., which deals with bilaterality of representation. It may, however, be pointed out that no other operative interference than that already described as necessary for cortex and nerve exposure having been performed, it is perfectly evident that if the stimulus was maximal, as it usually was in this experiment, a bilateral fit could and did happen, so that from one nerve an effect might be and was obtained due to discharge of both hemispheres.

It is, moreover, interesting from the point of view both of control and of localisation, that in cases where a strength of stimulus which did not evoke a general discharge was employed, whilst the application of the stimulus to the so-called lower limb area of the Cat produced definite electrical changes in the nerve, its application to the focus of representation of the upper limb evoked little or no change, even though the stimulus was followed by marked epileptic convulsions in the upper limbs. The localisation of the foci of representation of the movements of upper and lower limbs in the Carnivora, which has been determined by other observers, is thus corroborated by the use of the present method.

CHAPTER VI.—ON THE ELECTRICAL EFFECTS EVOKED IN THE SPINAL CORD AND MIXED NERVES BY EXCITATION OF THE CORONA RADIATA.

Excitation of Corona Radiata.

1. *Electrical Changes in the Spinal Cord.*

We will consider first the general character of the changes as evidenced by the movement of the capillary electrometer.

(*a.*) *Effects seen in Electrometer.*

The cortex and spinal cord having been exposed, the central end of the cord divided in the lower dorsal region was connected with the instrument in the manner already described, and the corona radiata displayed by the method detailed in Chapter III., Section 2.

We have already stated that it was early shown by François Franck and others that removal of the cortex and excitation of the corona radiata no longer gave the characteristic sequence of tonic followed by clonic muscular contraction, but simply a tonic contraction synchronous with the duration of the excitation, the first stage, as it were, of the cortical effect. In our earliest experiments (see 'Roy. Soc. Proc.'), we found that a similar difference occurred in the character of the electrical changes observed in the spinal cord, as evidenced by the capillary electrometer. The character of the change in the two conditions is well shown in the facsimile representations of the photographic records which are given in our former paper, the corona radiata effect being simply a persistent tonic negative variation, the amount of movement of the meniscus being about one division of the eye-piece scale.

The small size of the electrometer change, and the consequent difficulty of appreciating its comparative quantitative value under different circumstances, led us to employ the galvanometer as an index of its amount.

(*b.*) *Effects seen in Galvanometer.*

When the effect in the cord is observed with this instrument it is seen to be unlike that evoked by cortical excitation in this respect, that the deflection of the needle commences with the application of the stimulus, and ends sharply with its termination. The amount of the deflection is thus very definite, but of less extent than that obtained when the cortex is excited.

In the following table a series of observations made on three Cats are given, in which precautions were taken to insure that the state of anæsthesia, &c., should be in all cases as far as possible the same. The deflections vary from 37 to 175, the average being 102.

EFFECT in Spinal Cord.

	Intensity of excitation.	Duration of excitation.	Effect in spinal cord.	Character of muscular effect.
		Secs.		
Cat (99) . .	12,500	5	42	Tonic contraction
			37	,, ,,
			50	,, ,,
,, (288) . .	10,000	5	118	Well marked tonic contraction
			58	,, ,, ,,
			120	,, ,, ,,
			62	,, ,, ,,
	11,000	5	130	Well marked tonic contraction
			110	,, ,, ,,
			71	,, ,, ,,
			170	,, ,, ,,
,, (309) . .	8,000	5	125	Well marked tonic contraction
			175	,, ,, ,,
	8,000	5	135	,, ,, ,,
			129	,, ,, ,,
			15=1532	
		Average . .	102	

We would pass from this part of our subject, since our knowledge of the process of secondary degeneration has shown that in the arrangement of the experiment all we do is to observe at one (the spinal) end of a column of fibres the changes evoked by stimulating these fibres at the other (corona radiata) end, were it not that the above effect is capable of modification in a manner which demands consideration. Moreover, we wish to emphasise the fact, that in its simplest form the corona radiata effect, as observed in the cord, is an example of the application of the galvanometric method to the determination of directly continuous nerve tracts in the central nervous system. This, as we shall see later in dealing with the spinal cord itself, is one of the most valuable uses to which the method can be put. Thus when a definite tonic effect, and that only, is evoked by the excitation, the application of the stimulus to any fibres of the corona radiata, except those immediately underlying the focus of representation of the movement of the lower limb, produces no electrical changes in the lower dorsal cord, even though the muscles of other parts are sent into tonic contraction. The modifications we have referred to above, are those which have been observed by most workers with the graphic method, and consist in the presence of an after-effect in no wise differing from the clonic stage of the full cortical discharge save in duration and completeness. The assumption is naturally that in the arrangement of the experiment, it is impossible to avoid exciting association fibres (fibræ arcuatæ,

&c.), which arouse the neighbouring cortex cerebri, and cause a discharge from corpuscles in which the peripheral part under investigation is yet represented.

We have little doubt but that this is the true explanation, and believe that excitation really limited to the fibres of the corona radiata is never followed by such an after-effect. This will, however, be again referred to in Chapter VII.

2. *Electrical Changes in the Sciatic Nerve.*

As in the result of cortical stimulation, so in that of excitation of the corona radiata, there is a striking difference between the effect in the cord and that in the sciatic nerve. We have never yet observed any effect from the nerve when the electrometer was employed; in the galvanometer, however, such effects are generally seen, although the necessary stimulus has to be so strong as to run the risk of evoking discharge from the uninjured portions of cortex. Whenever such epileptic discharges obviously occurred, as evidenced by the muscular movements, the observation was regarded as worthless.

The following table gives the results observed in eight Cats, all those being excluded in which, owing to the degree of anæsthesia being less, the excitation brought about general muscular movements.

As in the case of cortical excitation, so here, the deflections observed in the (corresponding) nerve on the opposite side to that of the excitation are placed in a separate table to those observed in the nerve on the same side, the latter being given so as to show when bilateral effects were produced.

It will be seen that the amounts vary between 4 and 68, and that the average of all readings is 26.

ELECTRICAL Effects in the Nerve.

	Intensity of excitation.	Duration of excitation.	Effect in corresponding nerve.	Effect in nerve on same side.	Muscular effect observed.
		Secs.			
Cat (290) . . .	12,000	5	7	0	Tonus only
			9	0	,, ,,
,, (291) . . .	12,500	5	5	..	Weak tonus
,, (292) . . .	9,000	5	20	12	Good ,,
			18	..	,, ,,
	10,000	5	20	..	,, ,,
			6	2	,, ,,
,, (297) . . .	12,500	5	12	0	Good ,,
,, (298) . . .	12,000	5	4	0	Weak ,,
	12,700	5	11	0	Good ,,
,, (299) . . .	12,000	5	46	21	Powerful bilateral tonus
			61	26	,, ,, ,,
			10	0	Weak tonus
,, (303) . . .	10,000	5	30	12	Bilateral tonus
			28	14	,, ,,
			22	8	,, ,,
,, (305) . . .	8,000	5	52	14	Powerful ,,
			63	33	Bilateral ,,
			23	5	Feeble ,,
	10,000	5	59	25	Good ,,
			10	1	Very feeble tonus
			31	13	Fair tonus
			68	42	Bilateral good tonus
			23 = 615		
			26		

Special attention must be drawn to the fact that higher numbers than those given were sometimes obtained; however, these large deflections accompanied general movements of the animal, due, in part, to the fact that it is extremely difficult to maintain a proper degree of anæsthesia. If this is too slight, the stimulus causes a general awakening of the whole cerebral system.

The question of bilaterality will be referred to in the next chapter. It remains to institute a general comparison between the galvanometric effects observed in both cord and nerve when the cortex and corona radiata are respectively excited. Such a comparison will lead to a better understanding of the part played by the bulbo-spinal centres, though any complete inquiry into this difficult question must be postponed to Chapter XI., which treats directly of the matter.

If we arrange the parts of the nervous system here dealt with in their anatomical order, they form the following series :—

1. Cortex.
2. Corona radiata.

3. Spinal cord (dorsal region).
4. Bulbo-spinal centres.
5. Nerve.
6. Muscular nerve-endings.

The combinations of these parts involved in our experiments may be grouped as follows, and to each group is affixed the highest and lowest galvanometric reading obtained in the case of the Cat :—

Part stimulated.	Part observed.	Galvanometric effects.		
		Highest.	Lowest.	Average.
1–3. Cortex . . .	Dorsal cord . .	510	50	193
1–5. „ . . .	Sciatic nerve .	80	2	29
2–3. Corona radiata .	Dorsal cord . .	175	37	102
2–5. „ „ .	Sciatic nerve .	68	4	26

From these figures, which apply to the Cat only, it is very evident that the specific element distinguishing the cortex from the white fibres of the corona radiata leading away from it is the energetic discharge of its own structure, the corpuscles. Reverting now to the question raised at the beginning of this section, it is plain that the average amount of the effect produced by the corona radiata forms practically half, viz., 102, that, viz., 193, evoked by the cortex, the remainder naturally corresponding with the clonic after-effect. The levelling process effected by the block in the connection between the pyramidal fibres and the nerves through the corpuscles of the bulbo-spinal centres is so severe as apparently to reduce the increase due to the after-effect to too low an intensity to make itself felt in the galvanometer in any marked degree, for it will be seen in the above table that the figures for the sciatic nerve are practically equal.

Beyond multiplication of experiments to check and control these observations, we did not see that further investigation in this direction would be so profitable as examining the relations and action of the bulbo-spinal centres when separated from the cervical region of the spinal cord (see Chapters VIII., IX., X., XI.), since the phenomena of conduction in fibres are far more easily studied than those in which corpuscular mechanisms are involved.

CHAPTER VII.—ON BILATERALITY OF REPRESENTATION IN THE CEREBRUM, AS EVIDENCED BY THE ELECTRICAL CHANGES IN THE SPINAL CORD AND MIXED NERVE.

The galvanometric method affords an excellent means of determining to what extent any bilateral movements obtained in the lower limbs on exciting the cortex are associated with impulses proceeding down both sides of the cord.

It is obvious that a most important question is involved in this inquiry, that, namely, of the share taken in the production of bilateral effects by the different parts of the nervous system. When bilateral movements of the lower limbs are evoked by excitation of one cortex, it is conceivable (*a*) that in the portion of cortex excited, muscular movements on both sides are represented; (*b*) that the excitation has aroused the corresponding cortical areas in the opposite hemisphere, and thus produced the bilateral effect; (*c*) that the excitation has aroused the basal ganglia, cerebellum, &c.; (*d*) that the descending impulses, although unilateral when they come into relation with the spinal centres, are then brought into relation with both sides of the body.

In order to investigate this, the first problem to solve is that referred to last under (*d*). This, the present method, and that only is capable of doing, since by it we can determine the characters of the actual descending impulses in the cord before they come into relation with the bulbo-spinal centres. In this way we can ascertain to what extent the impulses which descend the cord from the brain already show a dual (bilateral) grouping.

We devoted a very large number of our cortical experiments to the further elucidation of this question, feeling that the great importance of any approach towards its solution, in consideration of its bearing upon the physiological characteristics of the cortical cells, was a sufficient justification.

It is necessary, before stating our results, to give a short categorical account of the work already done in this subject, and this is the more desirable since we cannot find any such *résumé* published.

Previous Work on the Subject.

The question whether both or only the opposite of the two sides of the body are represented in one cortex cerebri on the efferent or motor side has been approached experimentally by relatively but few authors.* As the results hitherto obtained do not by any means decide the important questions which offer themselves for solution,

* The subject has also been considered fully from the theoretical point of view by Broadbent ('British Medical Journal,' 1876, pp. 333, 401), this author believing that bilaterality of representation is always effected by commissures between the bulbo-spinal centres.

it is impossible to tabulate the facts in the definite manner used for the historical retrospect of the graphic and other methods.

Moreover, since the interpretation of the results is completely dependent upon the methods of experiment in each case, it will be better to arrange the facts as follows :—

(1.) Excitation experiments on the cortex.

(2.) Excitation experiments combined with division of commissures, *i.e.*, corpus callosum, &c.

(3.) Excitation experiments combined with the excision of the opposite "motor" area.

(4.) Excitation experiments combined with hemisection of the spinal cord or bulb.

(5.) Ablation of one hemisphere.

(6.) Ablation of the "motor" area of one hemisphere followed by ablation of that of the opposite side.

(7.) Excitation of the corpus callosum.

(8.) Degeneration of fibres after excision of portions of the cortex cerebri.

We will now briefly state the more important facts determined by the above methods of experiment, postponing for the present any criticism.

1. *Excitation Experiments on the Cortex.*

It was first observed by HITZIG,* later by FERRIER,† ALBERTONI,‡ and MUNK,§ and subsequently by FRANCK and PITRES,‖ that powerful excitation of one hemisphere in the Carnivora produced movement not only of the corresponding or opposite side of the body, but also of the same side as that stimulated.

FRANCK and PITRES‖ showed further that when the muscles of the same side were thrown into action they contracted ·01 second later than those of the opposite side, a most important observation.

BUBNOFF and HEIDENHAIN,¶ CARVILLE and DURET,¶ confirmed these facts.

JÄNICKE** observed that while in dogs bilateral representation of the facial muscles was very constant, in the limbs on the contrary, unilaterality was the rule, but that to this there were exceptions. His views were confirmed by UNVERRICHT.

LEWASCHEW†† noted that the movement on the opposite or corresponding side was a coordinated one (like a voluntary action), whereas that of the same side, besides being late, was only a simple tonus.

* 'Untersuchungen über das Gehirn,' Berlin, 1874, pp. 48, 134.

† 'Functions of the Brain,' 1st ed., 1874.

‡ 'Lo Sperimentale,' 1876.

§ 'Gesammelte Abhandlungen,' 1890.

‖ 'Compt. Rend. Laboratoire,' MAREY, 1878, 1879.

¶ *Loc. cit.*

** 'Centralblatt für klinische Medicin,' March, 1883, p. 177.

†† *Loc. cit.* See p. 346, *infra*.

Schäfer and Horsley* noted that bilateral representation of the facial muscles existed in various species of Monkey, but that the trunk and limb muscles were unilaterally represented.

Schäfer and Mott† confirmed these observations.

Beevor and Horsley‡ further showed in more detail that in the Bonnet Monkey (*Macacus sinicus*) the limbs were unilaterally represented, but that other groups of muscles, *e.g.*, the tongue, buccinator oris, &c., &c., were bilaterally represented in each hemisphere. They discuss this point also in another Paper on excitation of the internal capsule,§ and confirm the above statement relating to the trunk muscles.

Semon and Horsley‖ have shown that in all animals the vocal cord movements are absolutely bilaterally represented in the excitable area of the cortex; this bilaterality was previously observed by Krause in the Dog; it has been contested by Masini.

Brown-Séquard¶ in one experiment on a Monkey found that excitation of the gyrus fornicatus produced movements of the same side of the body, whereas excitation of the paracentral lobule immediately above evoked movement of the *opposite* side.

Asch and Neisser** found from (but a few) experiments in Rabbits that excitation of the cortex produced movement of the muscles on the same side, and, subsequently, those of the opposite side, whereas excitation of the corona radiata gave movement on the opposite side. The narcosis in their experiments was incomplete.

Couty†† occasionally also observed the same phenomenon exceptionally in Rodents, but only in the absence of narcosis. Steffahny‡‡ observed occasionally bilaterality of movement in Rabbits to follow excitation of one hemisphere. Braun§§ similarly noted bilaterality in the absence of narcosis.

2. *Excitation Experiments on the Cortex combined with Division of Commissures,* i.e., *Corpus Callosum, &c.*

Exner‖‖ observed that in the Rabbit, after section of the commissures, and even after ablation of one hemisphere (see No. 5), bilateral movements (nature not detailed, possibly tonus, p. 189 of his paper), occurred.

* 'Phil. Trans.,' B., 1888.
† 'Brit. Med. Jour.,' 1890.
‡ 'Phil. Trans.,' B., 1887, 1888, 1890.
§ 'Phil. Trans.,' B., 1890.
‖ 'Phil. Trans.,' B., 1890.
¶ 'Comptes Rendus de la Société de Biologie,' 1887, p. 261.
** 'Archiv für d. ges. Physiologie,' von Pflüger, 1887, p. 191.
†† 'Compt. Rend.,' vol. 96, 1883, p. 506.
‡‡ Eckhard's 'Beiträge,' 1888, p. 97.
§§ Eckhard's 'Beiträge,' 1876, p. 127.
‖‖ 'Wien, Akad. Sitzber.', 1881, 3 *Abth.*, p. 185.

François Franck and Pitres* found that in the Dog, after division of the corpus callosum, the anterior and middle commissures, or even the pons, "les réactions bilatérales" persisted (? tonus only).

Gliky† also found (see No. 4) bilaterality of movement after dividing all parts in the middle line to the mesencephalon, in the Rabbit.

Horsley‡ showed that in the Dog after division of the corpus callosum and commissures, as described by Franck and Pitres, although bilateral movements could be obtained upon excitation of one hemisphere, yet the movements were not the same in character on the two sides; the true cortical effect of tonus followed by clonus being only obtainable in the side opposite the excitation, whilst the effect on the same side was only a feeble tonus (*vide* also Lewaschew) and often absent.

3. *Excitation Experiments on the Cortex combined with Excision of the Opposite "Motor" Area.*

Franck and Pitres§ observed in the Dog the bilateral movements to persist (? tonus only on the same side) even after the opposite motor area had been removed ("centres corticaux opposés au centre excité"), and Exner‖ also in the Rabbit noted the occurrence of bilateral movements if one hemisphere were excited, even when the whole or major part of the opposite one had been excised.

Horsley¶ found the same in the Dog, but noted that while the limbs opposite (*i.e.*, corresponding) to the side excited developed the usual combination of tonus followed by clonus, the limbs on the same side exhibited only tonus. Further, that as in Nos. 1 and 2 the complete (tonic *plus* clonic) discharge from the cortex of one hemisphere could be obtained by adequate excitation without any bilateral movement whatever.

He also found the same to be true when the excitable region of one hemisphere was ablated and absinthe injected into a vein. In the resulting epileptic convulsion only tonus was noticeable in the limbs corresponding to the seat of ablation, whereas the typical tonus *plus* clonus was exceedingly marked in the limbs opposite the sound hemisphere. This differentiation was often very precise, *i.e.*, the tonus on the side of the sound cortex was very weak, even in the Cat.

In the Monkey the tonus mentioned was extremely slight, and possibly in Man is absent (Obre) under these circumstances.

* *Loc. cit.*

† Eckhard's 'Beiträge,' vol. 7, p. 179, 1876.

‡ 'Brown Lectures and Reports.'

§ See for full discussion François Franck: 'Fonctions Motrices du Cerveau,' 1887, p. 59.

‖ *Loc. cit.*

¶ 'Brown Lectures' since 1885; also, 'Reports of the Brown Institution.'

Semon and Horsley* observed that in all animals examined, *i.e.*, Rabbit, Cat, Dog, and Monkey, the bilateral movements of the vocal cords were still perfectly obtained on excitation of the one cortical representation after that of the opposite side had been removed.

4. *Excitation Experiments on the Cortex combined with Hemisection of the Spinal Cord, &c.* (Eckhard's *Method*).

Franck and Pitres† observed that in the Dog hemisection of the spinal cord on the same side as that of the hemisphere excited failed to abolish the bilateral movements in the limbs.

Lewaschew‡ followed the French authors by similar experiments in the Dog, from which he deduced the same idea, viz., that the bilaterality was accomplished by means of commissural fibres in the spinal cord.

Balighian§ observed that in the Rabbit the opposite, *i.e.*, normally corresponding, movements were not abolished by hemisection of the bulb opposite the lower border of the pons and on the same side as that of the hemisphere excited, whence he concluded that the crossing of the excitable fibres begins to occur as high as the lower border of the pons.

Balighian also showed that in the Rabbit, excitation of one hemisphere failed to elicit movement in the opposite limbs if the corresponding part of the spinal cord had been divided.

Schiff‖ found that in the Dog after section of the right crossed pyramidal tract excitation of the cortex with four Leclanché elements produced no result (whereas before the division this formed a maximal stimulus), and only with a current of fourteen elements were movements of both the hind limbs obtained.

Gliky¶ showed by hemisection of the bulb that in the Rabbit the pyramidal tract crossed below the centre of the fourth ventricle, and that a tendency towards unilaterality of representation prevailed.

Steffahny,** applying this method in Rabbits, came to the following conclusions: that the path of the crossed impulses for the innervation of the extensors of the fore limb is in the uppermost part of the cervical cord, the anterior column, and lower down in the lateral column, and further that there are paths for bilateral movements, and that these lie in close relation to those for the ordinary crossed effect.

* *Loc. cit.*

† *Loc. cit.*

‡ Pflüger's 'Archiv für die gesammte Physiologie,' vol. 26, 1885, p. 279.

§ Eckhard's 'Beiträge,' vol. 7, 1875.

‖ Pflüger's 'Archiv,' vol. 30, 1883, p. 248.

¶ Eckhard's 'Beiträge,' vol. 7, 1876, p. 186.

** Eckhard's 'Beiträge,' vol. 12, 1888, p. 43.

Schiff,* by limited section of the parts of the cord, was the first to find that after division of the crossed pyramidal tract in Dogs, no movement of the leg on the same side as the lesion followed upon excitation of the opposite excitable area.

Dupuy† stated that in the Dog opposed hemisections of the cervical region of the cord when separated from each other by about 1–1·5 cm. did not interfere with the production of movements in the lower limbs on exciting the cortex cerebri.

5. *Ablation of one Hemisphere.*

To test localisation in principle Goltz‡ has in the Dog removed large proportions of the brain, and recently§ succeeded in completing the ablation of one hemisphere.

The animal under these circumstances could walk, run, and use the limbs in all automatic movements of feeding, &c., there being no obvious persistent hemiplegia as in Monkeys and Men. For many weeks, however, there is in the Carnivora marked hemiplegia of the opposite side to the lesion (all authors), and according to Hitzig the loss of the "muscular sense" is permanent in these animals. This fact, as well as the concomitant persistence of anæsthesia to moderate tactile impressions, is also confirmed by the observations of Schiff, and one of us (V. H.).

Semon and Horsley‖ found that in all animals examined after removal of one hemisphere the "automatic" *i.e.*, respiratory, movements of the vocal cords were perfectly bilateral.

6. *Ablation of the "Motor" Area of one Hemisphere, followed by Ablation of that of the Opposite Side.*

Carville and Duret¶ investigated the matter by removing one so-called motor area, and observing the paresis caused thereby, noting that the paresis gradually disappeared as if by substitution on the part of the opposite sound hemisphere. Removal of this latter, however, did not reproduce the paresis of the limbs on the same side.

7. *Excitation and Degeneration of the Corpus Callosum.*

The results of excitation of the corpus callosum by Schäfer and Mott,** as well as the degeneration observed by Sherrington†† to follow localised ablation of portions

* 'Archiv f. d. ges. Physiologie,' vol. 30, p. 248.

† 'Compt. Rend. Soc. de Biol.'

‡ "Verrichtungen des Grosshirns." Pflüger's 'Archiv,' vol. 34, 1883, p. 50.

§ Demonstration at the 1st Internat. Physiol. Congress, Basle, 1889. See also the full account given by Langley and Grünbaum, 'Journal of Physiology,' vol. 11, 1890.

‖ *Loc. cit.*

¶ 'Archives de Physiologie' (Paris), 1875, p. 446, &c.

** 'British Medical Journal,' 1890; also 'Brain,' 1890.

†† 'Proceedings of the Physiological Society,' 1889.

of one cortex, suggest that the corpus callosum is a true commissure between the excitable or "motor" areas.

Brown-Séquard* had previously shown that the corpus callosum was excitable about its middle third, and he conseqnently regarded its fibres as commissural between the hemispheres.

8. *Degeneration of Fibres after Excision of Portions of the Cortex Cerebri.*

The phenomenon of bilaterality of function has also been referred to the normal exercise of those fibres which degenerate bilaterally (Pitres†) in the spinal cord after lesion of one hemisphere. Although the degeneration method has established completely the existence of such atrophy of channels in both lateral columns of the cord consequent upon a unilateral cerebral lesion, we do not, unfortunately, know whether these channels are "recrossed," as suggested by Sherrington,‡ Charcot, and others, or what is their destination, or whether they are to be regarded as of constant occurrence. As regards the latter point, it is certainly at present considered that they are not constantly affected by a cerebral lesion, and yet more rarely degenerate after a hemisection of the spinal cord. As yet, therefore, the method does not afford anatomical means of deciding the questions at issue.

Relation of the Foregoing Facts to our own Experiments.

In summarising the facts thus collated on this subject, it is difficult to avoid discussing the theoretical interpretations advanced by the authors quoted, but we do not think that anything is to be gained by such a procedure, and intend now to merely point out what conditions yet remain to be satisfied before anything like a full conclusion can be arrived at.

All agree that in the intact nervous system a nerve impulse from one hemisphere may readily pass to the other, excite it, and thus bring about bilaterality of movement as a result.

Nothing, however, can be judged as to such crossing to the other hemisphere being necessary for bilateral function until it is clearly defined in which part of the body such functional effects occur.

We must for this reason exclude altogether from the present discussion the facial movements, since these§ (see p. 344) are in great measure bilaterally repre-

* 'Compt. Rend. Soc. de Biol.,' 1879, p. 165; 1881, p. 204.

† 'Archives de Physiologie,' 1884, p. 142.

‡ 'Journal of Physiology,' 1885, p. 177. See also summary by Tooth: "Gulstonian Lectures on Secondary Degenerations of the Spinal Cord," 1889.

§ *Cf.* Paneth; also Unverricht.

sented in the excitable cortical areas of each hemisphere. The question, therefore, narrows itself down to that as to whether the highest, *i.e.*, purposive, movements of the *limbs* of both sides of the body are represented in the cortex of one and the same hemisphere. Theoretically, we are compelled to admit (following the teaching of HUGHLINGS JACKSON) from the evolutionary standpoint such bilateral representation of the limbs. The important point for experiment to decide, however, is whether such bilateral cortical representation exists in more highly differentiated animals to a sufficient extent to cause movements. The opinion of most authors is evidently that it does so exist. We feel, however, very strongly that the methods hitherto adopted by these authors are not definitive, and do not establish the positions claimed. We are led to this conclusion from the consideration of certain facts now to be discussed which have come under our notice in the present research, as well as of others previously discovered, the importance of which has of late become more recognised. By welding the fresh information, which the use of our method has given, to the old, we hope to help forward the solution of this apparently simple but very complex subject.

(1.) *Narcosis.*—As is seen from the foregoing retrospect, some authors have employed narcosis to a greater or less degree. The statement that a narcotised cortex could in any way "completely discharge" is always, of course, open to objection, and hence observations in animals narcotised to unconsciousness have been held by some to be incomplete. The answer to this objection, however, is simple and, we believe, sufficient; it is included in that of the next paragraph, in which "complete discharge" of the efferent apparatus of the cortex is seen to be effected even in unconsciousness. Clinical experience of epilepsy also affords evidence of the truth of this contention.

To look at the question from the opposite standpoint, although electrical excitation of the cortex is not in any way painful, still it is clear from observation of the influence of such stimuli in imperfect narcosis that the effect spreads rapidly from centre to centre, *i.e.*, to the opposite hemisphere, &c., and hence renders any topographical conclusions impossible.

The observations, therefore, which have been made in this way, though very valuable as throwing much light on synchronous excitation, *e.g.*, in epilepsy, &c., cannot, as yet, form a basis for the determination of the presence or absence of bilaterality of representation so far as the limbs are concerned.

(2.) *An adequate stimulus which completely discharges the cortex at one given focus of representation of one limb produces movement in that limb only and none in the limb of the same side.*

By the term "*adequate stimulus which completely discharges the cortex*" at one given spot, we mean an interrupted induction current of sufficient strength to evoke a strong movement in the limb represented (in the present research the leg), and to produce a slight excitation also (by overflow of nerve impulses) of the nearest lying centre or focus, which in our experiments was naturally that for the fore or upper limb. If the strength of the stimulus and the condition of the cortex be accurately

gauged beforehand, so that the latter is not thrown into a hyperexcitable state, then the above mentioned phenomenon can invariably be obtained, and this not only in the Monkey but also in the Cat. It might be objected that the cortex was not completely discharged, but we regard the overflow of the excitatory changes into the neighbouring foci as sufficient evidence of the required completeness. Moreover, the converse position, viz., the appearance of bilaterality tells the same (story see pp. 354 and 359), and thus forms the crucial argument.

If we are warranted, therefore, in our view that the cortex under these circumstances is completely discharged, the above described phenomenon negatives the practical existence of bilateral representation of the limb muscles in these animals.

(3.) *When ("bilateral") movements of both limbs follow excitation of one hemisphere after the excitable cortex of the opposite hemisphere has been thrown out of gear by ablation, division of the commissures, &c., &c., the movement of the limb on the side opposite to the cortex excited is the complete cortical effect of tonic followed by clonic contractions, whereas the movement of the limb on the same side as that of the cortex excited is only a tonic contraction.*

If bilateral movements of both limbs receive their originating impulses directly from one cortex, it is not comprehensible why the above-mentioned striking difference in the kind of movement of the limbs should exist. This difference, specially insisted on by one of us,* has been also observed by several authors (Lewaschew, &c.), and it suggests that the movement noted on the same side as the excitation is of some origin other than the cortex (its corresponding cortical apparatus being destroyed, be it remembered), for a simple tonus lasting during the excitation is characteristic not only of the cortex but of the cerebellar or other lower centres.

(4.) *When bilateral movements of limbs are observed, those of the limb of the same side as the cortex excited are always later in commencement than those of the opposite side.* (Franck and Pitres.)

This delay in movement of the limb of the same side is attributed by most to loss of time in traversing basal commissures. There is no means of testing this view except by some arrangement in which the exclusion of the said commissures is provided. As far as the commissures in the cord are concerned, this might be achieved by ascertaining the time relations of such excitatory electrical changes as will presently be shown to appear in each half of the longitudinally divided cord upon stimulation of the cortex.

(5.) *All experiments on this subject have included in their anatomical plan the cerebellum, without excluding its functional influence.*

In our own experiments about to be described, as well as those of the authors already quoted, the cerebellum has been left in normal connection with the central structures excited.

In performing the experiment of exciting one hemisphere after ablation of the

* V. H., *loc. cit.*

other, it is clear that the association through the superior peduncle of the cerebellum affords a means whereby the opposite lobe of that organ might be aroused, and so produce the tonic contractions of the limb on the side of excitation. This view is suggested to us more especially by the teachings of Dr. HUGHLINGS JACKSON, and it obviously must be excluded before a positive opinion can be expressed as to the bilateral representation of the limbs in the excitable cortex of one hemisphere.

From none of the foregoing researches can it be determined to what extent the bulbo-spinal centres are associated with bilateral movements, since in all experiments in which muscular contractions are taken as an index their functional activity is included.

Having laid before the reader these general considerations by way of preface, we will proceed to describe our own experiments, as far as they suggest fresh evidence for or against the different views just enunciated.

EXPERIMENTAL RESULTS IN CONNECTION WITH BILATERALITY.

The obvious elimination which the use of our method enables the experimenter to obtain is the removal of the influence of the bulbo-spinal centres.

This elimination is effected by the division of the spinal cord in the dorsal region, and the observation of the electrical changes occurring in its central end when the lower limb area of the cortex cerebri is excited. It is, however, essential to divide the descending tracts in the cord into two halves. This is done by splitting the cord longitudinally in its antero-posterior plane. The mode of operation employed has been described in Chapter III., Section 2,* and the preparation shown in Plates 31 and 33.

* It might reasonably be conceived that this operative procedure would seriously impair the conducting power of the cord. Although, as we point out in Chapter III., the posterior columns suffer somewhat, this is not the case with the lateral columns, the seat of the pyramidal tract to be investigated. An example of this is to be seen in the following case, where the effects in the divided cord of exciting but one hemisphere do not, when summed, fall far short of the effects obtained before the longitudinal section:

Cat. (324).	Part excited.	Duration of excitation.	Coil.	Part observed.	Galvanometer reading.	Muscular effect noted.
		Secs.			°	
Whole Cord divided and connected to galvanometer at 13th dorsal vertebra	Excitable area of left cortex	5	6,000	Whole cord	260	Slight fit
	,, ,, ,,	,,	8,000	,, ,,	340	Fair fit
	,, ,, ,,	,,	10,000	,, ,,	510	Powerful fit
Cord divided longitudinally and each half connected with galvanometer	,, ,, ,,	,,	6,000	Left half Right half	50 220	Good fit
	,, ,, ,,	,,	8,000	Left half Right half	45 195 210	,, ,,

As regards the method of observation, the electrical changes in each half of the longitudinally divided cord were recorded by means of the galvanometer, since it was essential to obtain results which admitted of relatively strict comparison as to their amounts. Each half of the cord was therefore attached to an independent pair of non-polarisable electrodes, and an arrangement made by which either pair could at any desired moment be switched into connection with the wires leading to the galvanometer, &c.

The result of this experimental investigation may be divided into groups, each one of which we must consider in detail.

I.—*Excitation of Cortex (whole Encephalon intact).—Electrical Changes in each half of Longitudinally Divided Cord.*

The cord having been divided, and split as just indicated, one cortical surface was exposed and the animal having been brought as far as possible into a perfectly steady, *i.e.*, constant state of narcotisation, the same strength of stimulus was then applied to the cortex, first one half of the cord being in connection with the galvanometer, and then the opposite half (see fig. 8). The results obtained, *i.e.*, from the opposite side of the spinal cord, and from the same side respectively, were then gathered together and averages taken.

It will be best to begin with the results of special experiments. Of these, the first we will refer to were made upon an animal (Cat 237), in which, from the movements of the upper limb, it was very easy to ascertain when the muscular contractions were unilateral or bilateral. It was seen that when the said contractions were strictly unilateral, the excitation of the hemisphere produced *no result* in the half of the cord on the same side, but a marked result in the half of the cord of the opposite side, viz., 275 degrees of the scale.

In this case complete unilaterality for the lower limb existed as far as the pyramidal tracts in the cord were concerned, for the cortex was, as we have before indicated in the first of our considerations, completely discharged, the discharge being evidenced by the large effect in the corresponding half of the cord, yet no electrical change could be seen in the other half indicative of descending impulses.

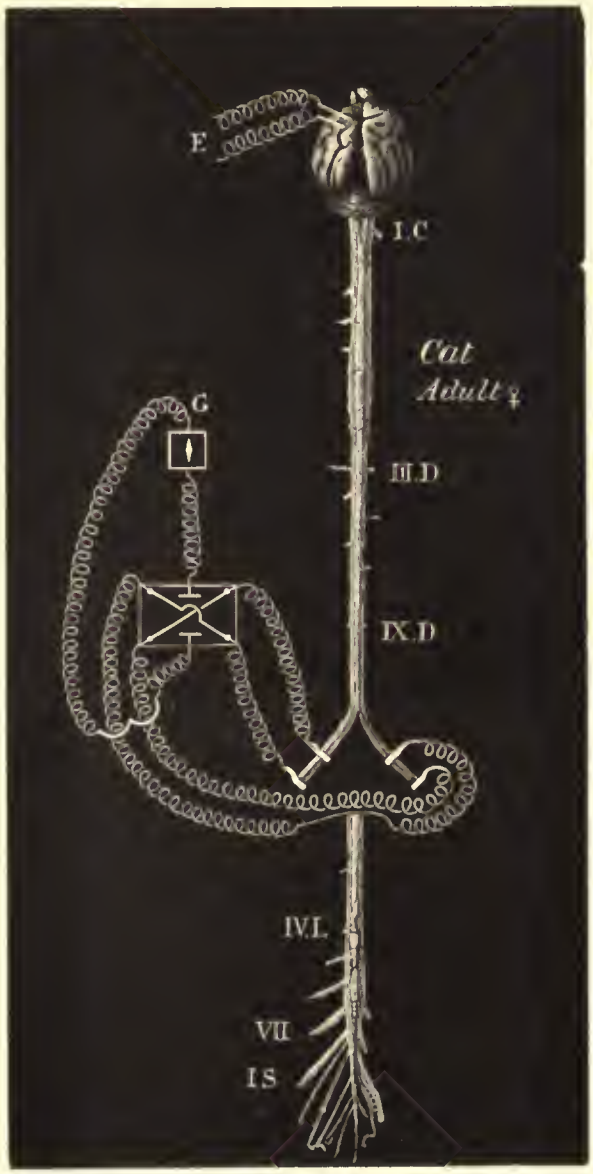
In another experiment made upon a Monkey (215), both cortices were exposed for excitation. In this animal, it was easy to confine the excitation apparently to one hemisphere, although, judging from the contractions of the muscles of the upper limb, the cortex excited was very completely discharged. In this instance, the cord was divided as described between the 10th and 11th dorsal nerves; the resting electrical difference of the two halves was in the proportion of two to one, the smaller being the right.

For the convenience of brevity, we will speak of the halves of the cord as the "right cord" and "left cord" respectively.

Excitation of the left hemisphere gave, with the coil at 5000, an effect in the right half of the cord of 425 degrees, and then, the right cord still remaining in connection

with the galvanometer, the right hemisphere was stimulated, the result being an effect of only 22 degrees. This last result, in addition to being only a twentieth of that evoked by the corresponding cortex was probably due to discharge from the left hemisphere, for, after the cortex had been allowed to rest, this pair of observations was

Fig. 8.



repeated with the following striking results, viz., the right cord being observed, the left hemisphere was excited, with a resulting variation of 365 degrees. The same cord being still led off, the right hemisphere was excited, *i.e.*, the hemisphere of the same side, and *no effect* was produced in the galvanometer. The same degree of narcotisation being maintained, and the same strength of coil being employed as that

just mentioned, viz., 5000, the left cord was then connected with the galvanometer; excitation of the right hemisphere (*i.e.*, that of the corresponding side) gave 375 degrees, and excitation of the left hemisphere (*i.e.*, that of the same side) only gave 8 degrees. This mode of pairing the observations is clearly one likely to give the most useful results, but we also paired the observations in the following way, viz., by connecting first one side of the cord with the galvanometer and then the other, in each case stimulating the same hemisphere.

The foregoing two selected experiments illustrate the conditions which are observed with the hemispheres in a normal state. Before considering the further evidence afforded by massing our observations, we must draw attention to the greatest difficulty in connection with this branch of enquiry, and which prevents us from speaking so positively upon this point, when the results noted at the beginning of any experiment are added to those recorded at the end. We refer to the great tendency of the cortex to become hyperexcitable after one or two excitations, and, consequently, for the excitatory state to pass from one hemisphere across to the other.

This is especially liable to occur when through repeated excitation the cortex has been thrown into a hyperexcitable state. This is, in fact, the objection which may be urged against any conclusions derived from massing together results, many of which being repetitions involve previous excitation. The same objection can also be urged with equal truth against the results of most of the observations of earlier experimenters; but upon the question whether this objection accounts for the whole of the results to be immediately given, we have no means of expressing any decisive judgment. It is, however, easy to understand that a considerable proportion of the bilateral effect noted in the two halves of the cord when all the results are taken may be due to this circumstance.

The average amount of the bilateral effect obtained in the two halves of the split cord when one hemisphere is directly excited is as follows:—

	Cord.	
	Opposite half.	Same half.
Cat—Average of 12 observations. . .	157	33
Monkey—Average of 31 observations .	158	32

It will be seen that when all results are averaged together there is an effect on both sides of the cord, and that its amount in the half opposite to the excited cortex is five times as great as that in the half which is on the same side.

The close identity of the figures in the two animals is remarkable, and not what our early observations had led us to anticipate.*

* One of us (V. H.), however, had already shown by experiments with absinthe combined with

The method under consideration, with both cortices exposed but intact, is not, however, favourable for testing bilaterality, since we have often had occasion to observe the great inequality in the excitability of the two hemispheres, which appears to be to a large extent connected with the necessary exposure of one cortex before the other.

From the result of other experiments we are inclined to believe that the effects (average 32) observed in the half of the cord on the side of the cortical excitation is due to the passage of impulses which have descended from the cortex opposite to that directly stimulated, but several interpretations are, of course, possible. In this connection it must be remembered that we do not yet know whether a *direct* pyramidal tract exists in the Carnivora (most authors denying its presence), and, further, that possibly even the galvanometer may not show an excitatory disturbance if the fibres by which the hemisphere of one side might be in relation with the same side of the spinal cord were very few in number.

II. *Excitation of Cortex.—Effect in Cord after previous Hemisection.*

The next step was to ascertain the effect of a previously performed hemisection of the cord between the encephalon and the observed region, the experiment being made with the view of eliminating any presumably crossed discharge from the cortex opposite to that excited.

The following experiment was made : In a Cat (225) the right half of the cord was divided under antiseptic precautions at the level of the lower border of the 9th dorsal vertebra. In this case there was well-marked motor paralysis in the right hind limb with rigidity, and diminution of perception of sensory stimulation of the same limb. The right knee jerk was exaggerated. When partly etherised the right hind limb became flaccid and the left somewhat rigid, the knee jerk then on the right side was greatly exaggerated and marked clonus present. These facts were noted just before the experiment now to be described. Eighty-four days later the cord was exposed and divided below the lesion, and the central end of the whole cord connected with the galvanometer electrodes. (See fig. 9.) The two cortices were then exposed and excited with an intensity of stimulus indicated by coil 8000 for 5 seconds.

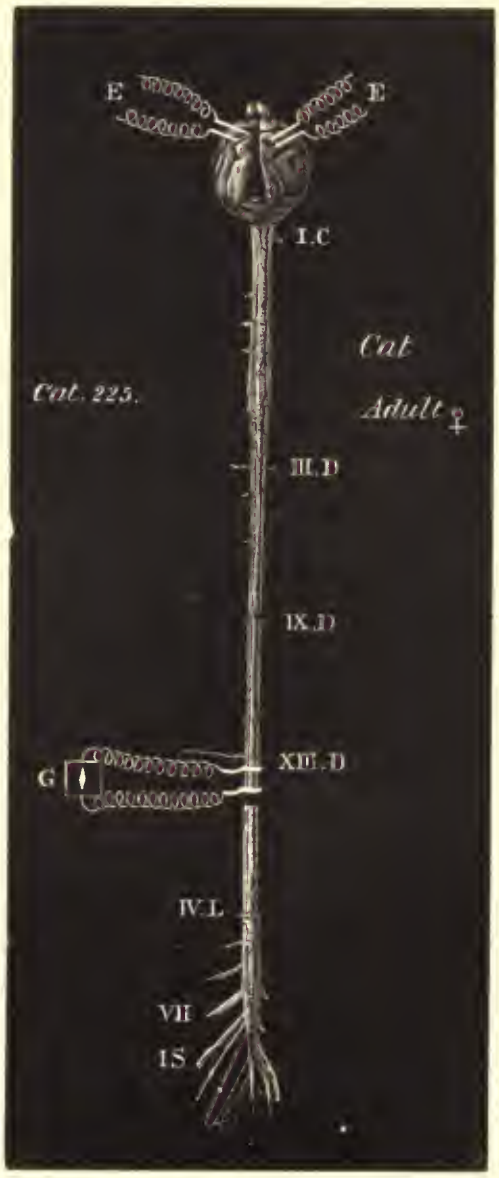
The following definite results were obtained :—

In the first place excitation of each hemisphere evidently produced unilateral epileptic fits. The effect in the descending (lower limb) fibres of the cord was as follows, it being remembered that the right half of the spinal cord had been divided. Excitation of the right cortex which produced unilateral fits on the left side of the body, gave a variation of 82 degrees in the galvanometer, whereas excitation of the left cortex, although it produced a good unilateral fit in the parts above the section, *i.e.*, right upper limb, gave nothing in the galvanometer, although the *whole* cord

ablation of one hemisphere or excitable area in Cats, that apparently in that animal complete unilaterality of the true cortical discharge (*i.e.*, tonus *plus* clonus) existed.

was the seat of galvanometric observation. In this way it was obvious that, when the excitation was so limited to one hemisphere as to produce only unilateral muscular movements, no impulses descended the fibres on the same side of the spinal cord

Fig. 9.



Note the hemisection of the cord on the right side at the level of the 9th dorsal vertebra.

and all impulses passed down the side opposite to that of the hemisphere excited.

That this conclusion was correct was confirmed by observing that even when on repeating the experiment a bilateral fit was obtained from stimulating either cortex,

whilst the cord effect evoked by the right cortex was increased to 134 scale, an effect was also evoked by excitation of the left cortex, though it amounted to only 15 scale.

The cord was next divided longitudinally and the electrical change observed on the two sides with the following result, it being remembered that the right half of the cord had been interrupted by the previous hemisection.

	Excitation.	Left half.	Right half.
Left cortex	6000, 5 secs.	trace	trace
Right „	„ „	50	
Left „	6500, „	trace	trace
Right „	„ „	215	
Left „	8000, „	5, 6, 20	
Right „	„ „	150	

It is clear from this that in the half of the cord (left) which offered an uninterrupted channel, the excitation of the cortex of the opposite side evoked large results, whilst the excitation of the cortex of the same side side evoked no results until a considerable intensity of stimulus was used and a bilateral fit produced. On microscopical investigation the lesion in the cord showed that the whole of the right half of the cord was destroyed, and the anterior third of the left posterior column, and the left posterior median. The descending degeneration, therefore, affected the right pyramidal tract in the lateral column only. The ascending degeneration affected both postero-median columns and the right cerebellar and antero-lateral tracts.

It should be mentioned that SCHIFF's observations on hemisections made just before excitation of the cortex show that the same relationships prevail as regards muscular movements.

III. *Excitation of Corona Radiata.—Electrical effect observed in each Half of Split Cord.*

The general electrical phenomena observed after excitation of the corona radiata, and especially as contrasted with those elicited by exciting the cortex are described in Chapter VI., but in attempting to still further elucidate the subject of bilaterality we arranged a third variety of experiment, originally designed for the graphic method by FRANCK and PITRES and others, viz., the investigation of the bilateral phenomenon noted after excision of the cortex, and consequent upon excitation of the subjacent corona radiata.

We have considered, on p. 338, the errors it involves, and have always endeavoured to minimise them as far as possible just as in the case of the cortex. Although the results are thus of necessity only to be accepted with reservations on the points already mentioned, which we must again briefly notice, nevertheless they do afford some very suggestive deductions.

We will first give the results obtained in the longitudinally divided cord by excitation of one corona radiata.

In this series of experiments we connected either half of the longitudinally divided cord with the galvanometer as in the cortex experiments previously described.

We have not yet seen any absolutely unilateral effect, as in the case of stimulation of the cortex. Very often the effect in the same side of the cord was extremely small (once only a trace), *e.g.*, 4°, 6°, 8°, &c., but it was always present. On massing the results together, *i.e.*, adding the observations in the Monkey to those in the Cat, we obtained the following proportionate averages :—

Half of cord on same side as excitation of corona—14° mean of 12 observations.
Half of cord opposite or corresponding to the corona excited—50° mean of 13 observations.

The proportion, therefore, is 7 to 2, whereas the cortex proportion is almost 5 to 1, and often purely unilateral. Consequently it appears that bilateral phenomena are more easily elicited by exciting the corona radiata than the cortex cerebri, provided the same care is employed to avoid as far as possible in both cases errors due to spread, &c.

The explanation of this is not far to seek, and, if correct, throws more light on bilaterality. It simply consists in the obvious fact that removal of the cortex lays bare a crowd of association fibres, the excitability of which is heightened by the section removing the cortex, and that it is the spread of the excitatory effect along these fibres to other central mechanisms in the encephalon, *i.e.*, opposite cortex, cerebellum, &c., which produces the bilateral phenomenon. It is thus extremely likely that bilateral tonus should occur after stimulation of but one corona radiata.

In accordance with what we have said before respecting the influence of ether, this reagent afforded an opportunity of testing the truth of the foregoing views, since the influence of bilateral central mechanisms could be by this means in part excluded, and it could therefore be seen whether or no there was a corresponding modification in the bilateral character of the effect.

We found that deeper etherisation invariably tended to restore in a great measure the inequality between the two cord effects, the difference between the two being much greater in proportion as the degree of anæsthesia increased. This again seems to indicate that any markedly bilateral effect is due to an additional functional activity in the cortex on the opposite side to the excited corona.

IV. *Excitation of Corona Radiata.—Effect in Cord with previous Hemisection.*

It was necessary now to repeat the design of the graphic experiments as employed by Franck, Schiff, Lewaschew, and others, using, however, our present electrical method, that is to say, observing how far a hemisection of the cord between the

encephalon and the part observed interrupted the propagation of impulses from the corresponding corona fibres.

The hemisection was made in the case (Cat 225) before referred to, p. 356, two months beforehand, at the 9th dorsal vertebra. For the observation the cord was exposed, divided, and split longitudinally at the level of the 1st lumbar vertebra. Both coronæ radiatæ were then exposed and excited alternately, the effects evoked being given below.

Excitation.	Cord.	
	Galvanometric effects.	
	Left half.	Right half.
Right Corona, 12,000, 3 seconds . . .	30	0
Left ,, ,, ,, . . .	Trace	0
Right ,, 13,000, ,, . . .	51	
Left ,, ,, ,, . . .	4	

In this case it is evident that the effect was almost completely unilateral.

In another case in which the hemisection was made at the time, there was no complete unilateral effect, but excitation of both coronæ elicited changes, the corresponding corona evoking an effect which was twice as large as that produced by stimulation of the one on the opposite side to the lesion. By means of etherisation the proportion was increased to 3 to 1, but since the alterations in excitability, due to the lesion being performed at the time, were disturbing factors, the influence of which could not be gauged, the experiment was not pursued further. It may be fairly concluded, however, that the more perfect the elimination of such complications, the more complete is the unilaterality of representation.

V. *Excitation of Corona Radiata after Complete Removal of one Hemisphere.—Effect in each Half of Divided Cord.*

In order to endeavour to ascertain whether the bilateral effect was in relation, not merely with the discharge of portions of the cortex of the hemisphere opposite to that of the excited corona, but also in relation with the basal ganglia and the cerebellum, we have in one animal (Cat 309) observed the influence of complete removal of one cerebral hemisphere.

The cord was, in this case, split longitudinally, and both coronæ exposed for alternate excitation, the results of several observations being given below.

Excitation of one corona.	Effect in opposite half of cord.	Effect in same half.
Right, 8000, 5 seconds	160	20
,, ,, ,, ...	61	8
,, ,, ,, ...	52	20
Left ,, ,, ...	54	34
,, ,, ,, ...	54	11
,, ,, ,, ...	50	25
	6 = 431	6 = 118
Average	72	20

The left cerebral hemisphere was now removed, and the effect of excitation of the right corona observed in each half of the cord.

	Opposite side.	Same side.
Right corona	100 75	27 30
	2 = 175	2 = 57
Average	87	28

The result is to show that the bilaterality continues, and apparently to the same extent as before.

The experiment is one which needs careful repetition, and special precautions to prevent errors.

VI. *Excitation of Cortex and Corona Radiata.—Effect in Sciatic Nerves.*

It has been already stated (Chapter V., Section 2, p. 332) that the excitation of the cortex evokes electrical effects in the sciatic nerves; and, further (Chapter VI., Section 2, p. 339), that similar effects are evoked by excitation of the corona radiata. A comparison between the amounts evoked in the nerves by excitation of one cortex, or by observation of the changes in one nerve consequent upon alternate excitation of each hemisphere, throws additional light upon the question of bilaterality of representation of the limbs now under discussion. It will be in the remembrance of the reader that the nerve effects derived from cortical excitation are remarkably small in

amount; in consequence of this, the comparison necessarily becomes less exact when the method of averages is used.

The following table gives this comparison in the case of six animals, four Cats and two Monkeys. In three cases, (*a*), (*b*), (*c*), the effect was observed in one nerve and each cortex alternately excited; in the remaining three cases, (*d*), (*e*), (*f*), the observations were made upon each nerve, one cortex only being exposed and stimulated.

	Intensity of stimulation.	Effect in nerve of opposite side.	Effect in nerve of same side.
(*a*) Cat (296)	11,000	5	0
		9	0
		12	0
		20	0
(*b*) Cat (290)	12,000	18	2
		10	0
		22	0
(*c*) Cat (298)	12,500	28	0
(*d*) Cat (299)	12,000	12	10
		20	0
		10	0
(*e*) Monkey (54)	5,000	16	5
		18	1
(*f*) Monkey (217)	5,000	18	0
		28	18
		16	5
		262	41
Average	..	16	2·5

From this table it is seen that, in the large majority of cases, unilaterality strictly prevailed. The small average amount of the bilateral effects, dependent, moreover, as it is upon a very few high readings, suggests that these results are due to that constant source of error in experiments upon bilaterality of representation, viz., hyperexcitability in other parts of the encephalon, produced by the operative procedure.

Examination of our records shows that when one corona is excited, and first one nerve and then the other connected with the galvanometer, the following average results were obtained:—

Corona radiata excited.

Average of all effects . Nerve opposite side 26 (23 observations).
Nerve same side 11 (20 observations).

This average, however, is the result of all the observations made, some of them being markedly bilateral in character. There are, however, no less than six cases in which no effect at all was observed on the same side as the excited corona,

and four cases in which the effect was under 10, and averaged only 4. It is, therefore, only by including cases of bilateral effects produced by powerful tonic discharges that the above total average is so comparatively high.

If, therefore, these higher figures were separated from the Table, we should find that the average effect on the same side would be not more than one-sixth of that on the opposite side; whilst, with evident and powerful bilateral discharges, the former effect amounts to one-half of the latter.

Summary of Facts.

The facts brought forward in the preceding pages seem to show that it is possible to obtain completely unilateral effects in both spinal cord and nerve when one cerebral hemisphere is excited, but that an increase in the intensity of the stimulus, and a diminution in the degree of narcosis, favour the production of bilateral effects—the inequality between the crossed and uncrossed effect becoming less and less marked in proportion as these favouring circumstances are augmented.

The conclusion to which the previous observations seemed to tend, that in one cortex bilateral representation of the limbs exists, does not seem to be supported by the present experiments, since such bilateral effects as may be witnessed are specially brought out by agencies which may be supposed to bring into play other portions of the central nervous system, particularly the opposite excitable cortex, the cerebellum, and basal structures. We feel, however, that without definitely proving this, our experiments have the result of making the question of bilateral representation in one cortex an open one, at least for the Carnivora.

To this position all we wish to add is our view that the weight of evidence goes to show that, where the excitation is properly limited to the cortico-pyramidal system, unilaterality of representation of the lower limb muscles appears to exist.

How far this is correct only further researches by the electrical method will, we believe, be successful in showing; and we hope that others will forward the investigation of this point.

CHAPTER VIII.—ON THE ELECTRICAL EFFECTS EVOKED IN THE SPINAL CORD BY THE EXCITATION OF THE VARIOUS PARTS OF THE SAME.

Section 1.—Introductory.
Section 2.—Propagation of Impulses by the fibres of the Cord.
Section 3.—General characters of electrical effects in the Cord following its excitation.
Section 4.—Excitatory electrical effects in the Cord, as evidenced by the Electrometer.
Section 5.—Electrical effects evoked by localised stimulation of the Spinal Cord; plan of experiments.
Section 6.—Electrical effects in the Lumbar Cord, following excitation of the Dorsal Cord.
Section 7.—Electrical effects in the Dorsal Cord, following excitation of the Lumbar Cord.
Section 8.—Electrical effects in each half of the divided Cord.
Section 9.—Influence upon electrical effects in the Cord of intervening sections of the various columns.
Section 10.—Summary of results of experiments.

Section 1.—Introductory.

The electrical changes produced in the cord by excitation of the cortex, and of the fibres of the corona radiata, whilst due to the passage of nerve impulses along tracts in the spinal cord, derive their interest from the further knowledge which they give us with reference to the functions of the excited parts in the encephalon from which those impulses spring.

It is otherwise with the material of this and the succeeding chapters; since the electrical changes, now to be described, are evoked by the excitation either of the different parts of the cord itself, or its nerves. The method of determining the characters of the functional activity of nerve tissue, by the study of those electrical effects which undoubtedly accompany and indicate the extent of that activity, is thus to be now applied solely with relation to the cord.

Since the functions of the cord are naturally divisible into those connected especially with its fibres—conductivity—and those connected especially with the activity of its cells, of which reflex action is the example, the present method was applied in any given experiment with special reference to the elucidation of one of these two branches of enquiry, it being always borne in mind that, as a matter of fact, the two groups of function overlap..

The question of the localisation of paths, in the fibres of the cord alone, has at present been only approached in reality by the method of histological experiment, including the embryological and degeneration methods, since previous physiological observation, relying on movement as an index, has always included the whole of the neuro-muscular mechanism.

The sole method for obtaining actual indications of the conduction of physiological processes in the fibres of the cord, is that of determining the presence in them of excitatory electrical changes. We have, therefore, carried out a very large number of

experiments upon the spinal cord under very different conditions, with the express purpose before us of obtaining data which should give clear evidence of the conduction of nerve impulses in its fibres and centres respectively. The results furnished by our experiments may be split up into the following groups :—

A. The experimental evidence of definite localisation of the channels of conduction of nerve impulses afforded by electrical changes in the cord, when evoked by stimulation of its different parts, whether distal or proximal.

B. The evidence of the localisation in the cord of fibres which enter it by the roots afforded by electrical changes in the cord when evoked by stimulation of its nerves.

C. The evidence of the relations of the spinal cord to the nerves afforded by electrical changes in the nerves, when evoked by stimulation of separate parts of the cord.

D. The experiments elucidating the complicated group of phenomena in relation with the reflex activity and function of the spinal nerve cells. This may be expressed as follows :—

The evidence afforded by the electrical changes, in both cord and nerve, of the nature of the rôle of the nerve corpuscles in the cord.

To obtain a sufficient mass of evidence, to establish even a few conclusions in these four subjects, a large number of experiments have been carried out, constituting by far the larger share of the work we have done since our preliminary communication in the ' Proceedings of the Royal Society,' in 1888.

The groups of data just indicated, in which these results are expressed, will be treated of in the succeeding four consecutive chapters; group A. in the present Chapter VIII., B. in Chapter IX., C. in Chapter X., and D. in Chapter XI., this being the order which seems to us at once the most natural and the most likely to present the conclusions in a logical and thus intelligible manner.

We therefore now pass to the consideration of the experiments, confining ourselves in this chapter to the electrical changes evoked in the spinal cord by stimulation of its different parts, and these only.

It is, however, first necessary to say a few words on the general question of conduction in the nerve fibres of the cord.

Section 2.—Propagation of Impulses by the Fibres of the Cord.

It has been maintained that the nerve fibres of the spinal cord do not respond to direct stimulation, in the same way that the fibres in a mixed nerve do,* and that it is the cellular elements alone which respond to excitation, the resultant nerve impulses being therefore, according to this view, indirect. The experiments to be detailed in this and the succeeding chapters will give convincing proof, if that is necessary, of the

* Van Deen, ' Nederl. Tijdschr. v. Geneesk.,' vol. 3, p. 393. Moleschott, ' Unters. z. Naturl.,' 1860, vol. 7, p. 380.

erroneous character of this view. The nerve fibres in the cord respond to direct excitation, like those in the nerve roots and nerve trunk ; that is to say, nerve impulses, with their accompanying electrical effects, are propagated in both directions along any *continuous* nerve fibres which may exist in the excited area; but, in addition, complications are introduced by the connection of a large number of the fibres with nerve cells, this connection causing now a possible decrease in the total electrical effects, presumably by the blocking of the path and the falling out of certain impulses, now an increase, presumably by the awakening of cells which lie in the path, and the accession of fresh impulses generated in these structures.

We will first state in general terms upon what facts rests our present knowledge of the mode of propagation of nerve impulses, from an excited area of the cord along continuous paths to a distant unexcited area.

(*a.*) It has been already pointed out in the historical introduction that the methods of histological investigation, particularly those associated with the presence of developmental and degenerative changes, have unravelled from the skein of nerve fibres in the cord certain tracts, and grouped them into columns of a continuous character in the lateral and posterior regions respectively. The limits of our knowledge have already been alluded to, but the inadequate character of the method is shown by the large number of fibres which are displayed in each transverse section of the cord, and the comparatively small number as to which a continuous connection with other parts of the cord has been demonstrated.

(*b.*) When we turn to the results of physiological experiments, the only method which has furnished satisfactory indications of direct physiological continuity in a tract of nerve fibres is that employed by Woroschiloff, Schiff, and others, of exciting the peripheral end of the cut cord below the medulla and observing the muscular movements of the lower limbs, in one case with the lower part of the cord intact, in another with a section of some structurally known column. In this way it has been shown that a group of fibres in the lateral column forms a path of such direct continuity between the seat of excitation in the cervical region and the lumbar cord that its section interrupts the passage of the descending nerve impulses generated in the former region, and it is therefore inferred that this path is, physiologically speaking, directly continuous.

(*c.*) Another method of determining the character of propagation in the spinal paths is the classical method employed by Helmholtz in the case of the nerve trunks, that is, the measurement of the transmission time. This, in the case of the fibres in the nerve trunk (Frog, Rabbit), is generally held to be about 33 metres per second, though in Man the conduction along sensory fibres is stated to be twice as fast. The experimental determination of this latter is, however, complicated by the methods used, which include the measurement of the individual reaction time, and introduce, therefore, additional uncertain factors which blur the clearness of the results.

Similar attempts have been made to determine the rate of conduction of nerve impulses in the spinal cord, both centrifugal and centripetal in character. Most of the experiments have been made upon Man by measuring the reaction time, and are therefore more or less untrustworthy owing to the conditions just mentioned. EXNER* obtained thus a mean result for centrifugal impulses of 11 to 12 metres in 1 second, for centripetal impulses of 8 metres. On the other hand, VON WITTICH,† by the use of a similar method, had previously obtained a rate of 26 metres for the centrifugal impulses. We have been unable to find any description of observations upon the Cat with regard to conduction, though such might easily be carried out by the use of the graphic method, and since it was important for us to know the behaviour of the fibres in the cord in this respect, we devoted a few preliminary experiments to the determination of conduction time only.

These experiments may be briefly described as follows:—

The cord was exposed in the anæsthetised animal in the lower cervical and lower dorsal regions respectively; the rectus femoris muscle was then selected for graphic record. The advantages offered by this muscle are—

(1.) Its anatomical relation with the pelvis, enabling the leg and trunk to be fixed, and the muscle brought out at right angles to the body.
(2.) The ease with which it could be separated from the surrounding parts.
(3.) Its own structure—that of a long thin muscle, with parallel fibres.

The lower tendon of the muscle was divided and ligatured; the ligature was then attached by means of a pulley to the lever of TIGERSTEDT'S break key,‡ so adjusted that the smallest contraction of the muscle was sufficient to raise the lever, and thus break an electrical contact. This contact formed part of an independent circuit, including one of SMITH'S new chronographs§ and three storage cells; it was ascertained that the movements of the chronograph armature occurred within 3/10000 second of the break of the circuit.

The movement of the chronograph lever recorded upon the travelling glass plate of a spring myograph (*Federmyographion*), the rate of movement being 25 centims. in 1/100 sec. The lateral column of the exposed cord was excited by a single induction shock, which was obtained by allowing the traveller to break, at a given point of its course, the primary circuit of a KRONECKER'S inductorium. As the moment of break was always the same, the break induction shock obtained was uniform in all cases, both as to intensity and time of occurrence; the position of the secondary coil was 2000.

The following measurements were obtained of the duration of the period between

* EXNER, PFLÜGER'S 'Archiv,' 1873, vol. 7, p. 632.
† v. WITTICH, 'Archiv f. Pathol. Anat.,' 1869, vol. 46, p. 476.
‡ *Loc. cit.*
§ *Loc. cit.*

excitation and commencement of muscular response, when the former occurred at the level of the 5th cervical and 2nd lumbar nerves respectively :—

Cat (163).

Excitation at 5th cervical.	Excitation at 2nd lumbar.	Difference.
·0217	·0170	·0047
·0210	·0170	·0040
·0217	·0172	·0045
·0241	·0200	·0041
Average ·0221	·0178	·0043

The distance between the 5th cervical and the 2nd lumbar was found to be 17 centims., and since the average difference of time between the muscular response evoked by the excitation at the two regions is ·0043, this difference indicates that the cord delay is such as would be caused if the nerve impulses starting from the cervical region travelled along the cord at 39½ metres per second. This experiment, therefore, seems to show that the time occupied by the conduction of nerve impulses in the Mammalian cord closely resembles that occupied by their conduction in nerve trunks; and it confirms the view that there is an efferent path in the cord leading from the cervical to the lumbar region in which a physiological continuity exists similar to that which forms the basis of nerve conduction in the fibres of mixed nerve trunks.

It will be noticed that the more exact physiological methods just referred to rely upon the observation of muscular movements. This involves serious disadvantages, since, in the first place, the method is thereby limited to the efferent fibres, and thus the physiological scope of any inquiry is narrowed; whilst, in the second place, the structural connections between the efferent fibres in the cord and the anterior roots of the nerves is to a great extent unknown, and certainly involves cellular elements, thus introducing new physiological conditions.

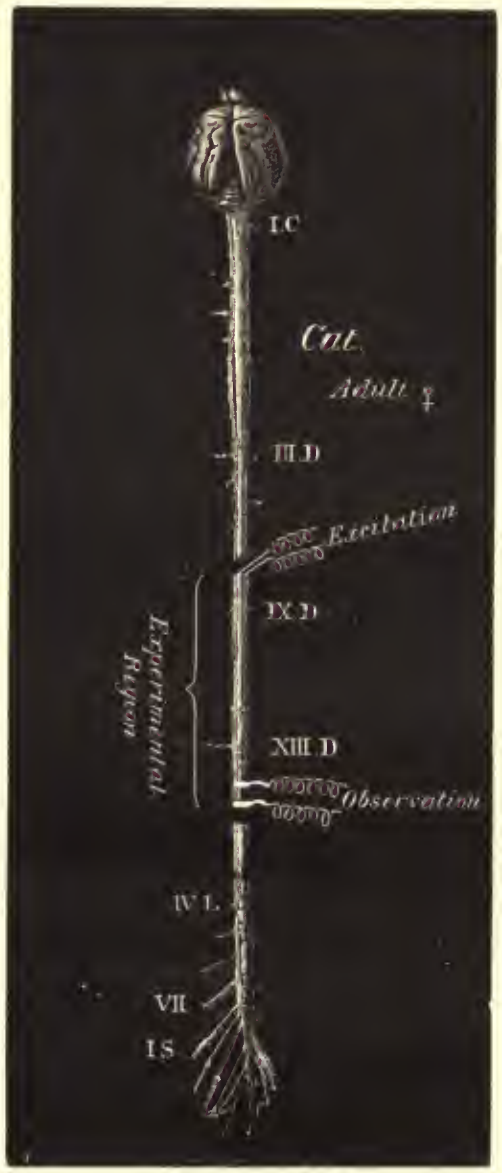
There is, as it seems to us, only one line of experimental enquiry which is free from these objections—that, namely, of ascertaining the existence of the nerve impulses in the fibres of the spinal cord itself, through careful quantitative observations of the electrical effects by which they are accompanied.

The present chapter will be devoted to the consideration in detail of the results of such observations in the dorsal and lumbar regions of the cord respectively. The novelty of the method, and the important bearing which the results have upon the physiology of the cord, we trust will warrant this extended treatment.

Section 3.—General Character of the Electrical Effects in the Cord.

The earliest experiments we made upon the cord showed that pronounced electrical changes always occurred in any portion of the lower dorsal and lumbar regions when some other portion in continuity was excited electrically. The simplest method of

Fig. 10.



excitation was that of inserting needles into the cord, the needles being connected with wires attached to the secondary circuit of the inductorium. It is obvious that if the excitation was carried out upon the cord whilst still in connection with the cerebrum, any resultant effects in the former would be the sum of the direct excitatory

changes and those indirectly produced by the reflex discharge of the cortex, as described in the preceding chapters. To avoid this and to obtain uncomplicated effects the cord was always severed from its connection with the higher centres.

The plan followed in the experiment was, therefore, as follows: two situations were selected, in almost all cases about the level of the 8th dorsal and 2nd to 3rd lumbar vertebræ; the cord was then first exposed for a short distance at the upper one and divided. It was then carefully exposed in the lower region and divided again, the upper division being made first in order to diminish, by cutting off all connection with the higher centres, the shock which subsequent operations necessarily involved. The portion of cord (see fig. 10), included between the upper or 8th dorsal section and the lower or 2nd lumbar one, formed thus an isolated fragment, and since it was upon this portion that the experiments to be detailed were carried out, this fragment may be termed the "experimental region" of the cord. A portion of this experimental region was always prepared for observation at either its dorsal or lumbar end, the preparation consisting in the exposure of from 4 to 5 centims. of the cord in immediate connection with the cross section and the division of all root and other attachments. The cut end of the portion was then ligatured, and the prepared part raised from the canal and suspended in air, care being taken to avoid all undue pull upon the structure. As previously described, (see Plate 29) the trunk was immovably fixed by holding the vertebræ in the ivory jaws of a clamp, which was rigidly attached to a metal rod fixed into the experimental table.

The ligatured end of the cord thus freed was attached by the before-mentioned cables of thread soaked in ·6 per cent. NaCl solution and plastered with kaolin, to the galvanometric non-polarisable electrodes, one cable being tied round the ligatured end and cross section, the other round the longitudinal surface about 1 centim. distant.

The usual resting difference between the surface and cross section was found to be present in all cases, and was always kept carefully compensated; its characteristics have been fully gone into in Chapter IV., and it will therefore not be further alluded to here.

If the other exposed end of the experimental tract were now excited, either by thrusting through it a pair of needle electrodes, or by placing upon the cut end the points of a pair of ordinary platinum electrodes, an excitatory electrical effect was seen in the portion connected with the galvanometric electrodes. This effect is always of such a character as to be opposed to the resting difference; it is suddenly developed with the commencement of the stimulation, and subsides on its cessation, being followed by the rise in the resting difference which is described in Chapter IV. It is evidenced both in the galvanometer and the capillary electrometer, the amount of deflection of the needle and of movement of the mercury being dependent upon (1) the nature, intensity, and number of the successive stimuli, (2) the condition of the animal.

(1.) *Relation of the Effect to the Stimulus.*

A. *Nature of Stimulus.*

(*a.*) *Single Induction Shock.*—The effect can be evoked by a single stimulus, but in that case gives only slight deflections in the galvanometer, but appreciable movements in the electrometer. Thus, in one experiment (Cat 122) in which the dorsal end of the experimental tract was connected with the non-polarisable electrodes and the lumbar end with needle electrodes, on excitation by a single break induction shock the electrometer showed a sudden transient movement of the mercurial meniscus of considerable size, seven divisions of the eyepiece scale; with the single make shock, a movement of five divisions was observed, both movements being opposed in direction to that produced by the resting difference.

(*b.*) *Repeated Induction Shocks.*—When the cord is excited by a rapid succession of equal and alternately directed induction shocks, more pronounced electrical changes are produced in the cord; the amount of the galvanometric change becomes very appreciable, amounting in some cases to two or three hundred scale, the amount of the effect in both the galvanometer and the electrometer varying with the intensity and direction of the successive stimuli. The best general idea of this effect is obtained with the latter instrument. The mercury is seen to leap at the moment of excitation in a direction opposed to that of the movement previously due to the uncompensated resting difference, this sudden change of level amounting to from 10 to 15 divisions of the eyepiece; it then slowly continues to rise until the successive stimuli cease, when a rapid subsidence to rather below its original level occurs.

(*c.*) *Mechanical Stimulus.*—If with one end of the experimental tract in connection with the electrodes the other end receive a sudden mechanical stimulus, an electrical effect is evidenced in both galvanometer and electrometer. The most effective mechanical stimulus is that of sudden complete division or squeezing of the end of the cord; for this purpose ivory scissors were first used, but we afterwards found that if insulating precautions were taken, sharp metal scissors could be employed with more advantage, since the keenness of the blades ensured a clean cut and avoided the dangers due to dragging on the cord. Such a division produces a small deflection of 20 to 30 scale in the galvanometer, and a pronounced movement of from 5 to 7 (eyepiece divisions) of the mercurial meniscus.

After injection of strychnia, the slightest mechanical irritation of the cord or sensory impression evokes marked electrical effects in the galvanometer and electrometer.

B. *Intensity and Number of Stimuli.*

Other things being equal, the cord electrical effect varies directly with the intensity and number of the successive stimuli, a limit being reached in this respect, the change

being conditioned in the same general way as is the well-known electrical effect in the excited Frog's nerve.

As far as the galvanometer is concerned, since the falling time of our instrument was 10 seconds, the effect for successive stimuli kept up for less than 10 seconds must be obviously directly proportional to the time, hence, in all exact experiments involving this instrument, it was essential that the duration of the period of stimulation and the number, therefore, of the successive stimuli used should be the same. This was effected by the revolving paraffin key described in Chapter III., which ensured a strictly uniform period.

(2.) *Condition of the Animal.*

A. *Anæsthesia.*

The character of the effect in the cord, unlike that in the nerve, is varied not only by the intensity of the stimulus, but also by the introduction of changes in the condition of the animal. These are connected with the awakening of the central cellular elements of the cord through the intensity of the stimulation used. The condition of the animal largely affects the limit of intensity at which any stimulus becomes adequate to arouse these corpuscular elements. Thus if profoundly anæsthetised a strong stimulus is necessary, but if the narcosis be but slight, a weak stimulus may evoke the result.

Although the subject of anæsthesia has been already referred to in Chapter III., it has such an important bearing on the present results that it must be reintroduced at this juncture. Our experiments abound with instances of the following character: in a Cat (371) the lower (lumbar) end of the experimental tract was connected with the galvanometer, and the lateral region of the cord in the upper dorsal section was excited with a series of 500 successive equal and opposite induction shocks (100 a second for 5 seconds). The galvanometric effect obtained was a deflection of 230 scale, the anæsthesia though complete as regards consciousness being of a comparatively slight character. The ether was now pushed and the anæsthesia made more profound, abolishing reflex movements, when the effect of a precisely similar excitation was indicated by 142.

In another animal (Cat 375) electrical effects similarly produced in a state of profound and slight anæsthesia show, when compared, the same differences, both with minimal and maximal intensities of stimulus.

	Profound anæsthesia.	Slight anæsthesia.
Cat (375)		
(Stimulus 500 minimal) .	60 galvanometric scale degrees	190
	82 „ „ „	140
	98 „ „ „	215
(Stimulus 1000 maximal) .	192 „ „ „	243
	273 „ „ „	295
	165 „ „ „	210
	295 „ „ „	410

Thus the degree of anæsthesia in which the animal happens to be influences the result very considerably, and is a convincing proof of the true physiological basis of the cord electrical effect, viz., that it is dependent upon the number and intensity of excitatory impulses in the observed region. It may be pointed out once more that this influence of anæsthesia is also sufficient to show, what might perhaps be otherwise suspected, that there is no objection to the use of the electrical method of stimulation through its possibly involving errors due to electrical escape.

Further proof that with the method of isolation used no such escape occurs is shown by the similarly directed effect evoked by both the make and break induction shocks, and by the production of the effect by mechanical stimulation. A still more convincing proof is, however, the complete disappearance of the effect on systemic death. (See Chapter III., section 4.)

B. *Systemic death and injury.*

The influence of systemic death upon the physiological condition of the spinal cord has been already referred to in connection with the resting difference. It was there stated that the difference keeps up and increases in the exposed portion of cord as long as it is in connection with a part which through the maintenance of an unimpaired circulation retains its normal state of nutrition. When systemic death occurs the difference immediately begins to fall, and in a very few minutes (2–5) the excitatory electrical effect disappears, the loss of excitability occurring in the case of the spinal cord with much greater rapidity than in the case of the sciatic nerve.

This disappearance occurs without systemic death if by any movement of the animal the cord is pulled upon, or if it is bruised in preparation at a point intervening between the seat of excitation and that of observation. Finally, the functional endurance of the tissue is dependent upon the animal used, differing in different species and in the different animals of the same species.

The most important general conditions by which the cord electrical effect is controlled, having been thus set forth, we pass on to consider what information a detailed examination of the characters and amounts of the electrical effects evoked under different circumstances, furnishes as to the structure and functions of the spinal cord.

In our earlier experiments we made use of the capillary electrometer, and we will, therefore, first briefly describe those made with this instrument.

Section 4.—Excitatory Electrical Effects in the Cord Investigated by Means of the Capillary Electrometer.

The electrometer, owing to the rapidity with which the mercury moves, furnishes valuable information as to the alterations in character and amount of electrical changes which follow one another in rapid succession. We have already indicated the experimental advantages which this confers in the examination of the cord effects evoked by cortical stimulation.* Since, however, the conditions which increase the sensitive characters of the instrument are to a great extent those which diminish its rapidity, it is almost impossible at present to obtain an instrument of sufficient sensibility for our purpose, without so slowing its movement that it takes more than $\frac{1}{15}$ second for the mercury to complete its rise or fall. If, therefore, a series of transient electrical changes similar in direction, following one another at intervals of less than $\frac{1}{15}$ second and all of equal intensity, are allowed to affect the instrument, then since the movement of the meniscus due to the first change would take $\frac{1}{15}$ second for its completion, the second change will occur when the mercury is either in movement or has just completed its excursion and not returned; a second movement is thus super-imposed on the first; so a third on the second, until a limit of fusion is reached, this being dependent upon the fact that with each additional displacement the counter-pull of the surface tension increases, and finally the displaced mercury is maintained at a new level without any additional displacement perceptible on either side of the level attained. It is probable that an extremely fine vibration synchronous with the rate of successive electrical effects exists, but when the successive electromotive changes are uniform in amount, direction, and time relations, such a vibration must be extremely small.

A very different condition is introduced when these electrical changes are alternate in direction, since now each displacement by one effect, whilst still in progress, is counteracted by another in the reverse direction due to the succeeding change being of opposite sign to its predecessor. The effect of such a series of electrical changes even when following one another at such short intervals as $\frac{1}{100}$ second is thus clearly visible, whatever level the mercury may have reached, as a blurring of the edge of the meniscus. The appearance to the eye may be described as a grey border to the otherwise black opaque column when viewed under the microscope.

This peculiarity of the electrometer at once enables us to judge whether, in a series of brief electrical changes, these are similar or dissimilar in direction, and we will first draw attention to this point in connection with the electrical effects in the spinal cord.

* See this paper, p. 324, also 'Roy. Soc. Proc.,' Nov., 1888 (vol. 45, p. 18).

The present series of experiments being planned for purposes of quantitative measurement, the least complicated and most constant conditions were in all cases selected, these being associated with careful isolation, and with the presence of one electrode only in contact with the natural surface. It is probable that with these conditions the total excitatory electrical change in the electrode circuit is chiefly that produced by alterations affecting this one electrode.

We will now proceed to describe the character of the movements of the mercury when, with the capillary electrometer connected by the electrodes with an isolated portion of cord, this structure is stimulated by a series of induction shocks alternate in direction and following one another at intervals of $\frac{1}{100}$ second (Helmholtz side-wire inductorium).

It has already been stated that one end of the "experimental tract" is prepared for connection with the non-polarisable electrodes, the other for excitation; so far as the character of the effect revealed by the electrometer is concerned, it makes no appreciable difference which end is respectively used for the purpose. In both cases a minimal excitation evokes an electrical change in the other end of the tract which affects the mercury of the electrometer, so that it moves rapidly up to a certain point, and there remains steady without visible oscillation, while it falls on the cessation of the stimulus, the mercury rapidly returning to its previous resting position.

With more intense stimuli a larger excursion of the mercury is obtained, and although no evidence of rapid vibration is detected, the character of the movement often becomes irregular, rising and falling at intervals in a more or less abrupt manner.

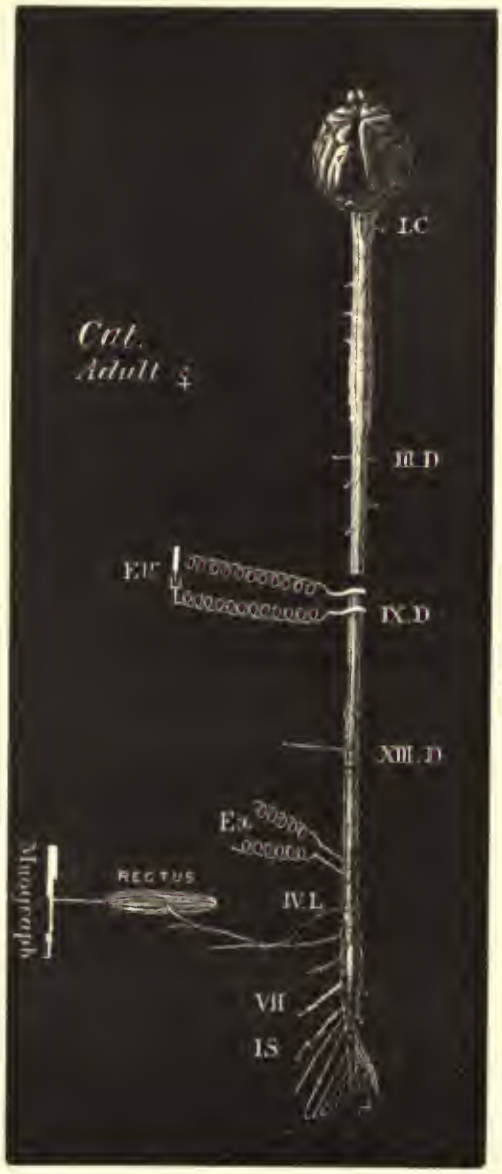
Whilst then it was clear from its character that the movement of the mercury is in no way connected with any electrotonic or other escape from the exciting circuit, since there is no evidence of rapid rhythmical alternating effect, synchronous with the number of stimuli, it was desirable to ascertain to what extent the irregularities just referred to were true indications of changes in the cord.

To ascertain this, experiments were made in which (see fig. 11) the cord was divided at one point only, the 8th dorsal, and the upper end of the lower fragment connected with the electrometer. The rectus femoris muscle was then prepared as indicated in the preceding paragraphs dealing with the transmission time (p. 366), but the attached ligature was fixed to a strong spring (Fick's isometric myograph), the movements of which, as recorded by a lever, were magnified 50 times. The cord was then exposed in the lumbar region and its lateral surface excited, the muscular contractions were observed and recorded, and at the same time the character of any displacement of the mercury of the electrometer was ascertained as far as possible by the eye, and roughly drawn upon paper.

It was thus ascertained that the electrical effects in the dorsal region of the cord evoked by lumbar excitation, and evidenced by the mercurial movements, coincided in plan and character with the muscular effects.

Since the electrical changes evoked by excitation of the cord thus appeared to afford true indications of the passage of nerve impulses along its nerve fibres, it seemed to us quite possible to obtain for any one set of fibres a measurement of the value of the electrical effects in it which would bear comparison with a similar measurement

Fig. 11.



obtained in the case of some other set. By piecing together the information thus obtained, and by varying the conditions in which the cord was placed, we hoped to determine the comparative number or at least resistance of the channels along which excitatory impulses are propagated from the excited to the observed area. Further, by means of carefully planned interruptions, we hoped to ascertain how far such impulses

were limited, presumably by the anatomical relations of the paths along which they were conducted, to given tracts of fibres in the different columns. We thus designed our work to ascertain the scheme upon which the fibrous structure of the cord was arranged, and this for both ascending and descending impulses.

We found that the electrometer was not a suitable instrument for this investigation, since with minimal stimulation its movements were too small to admit of sufficiently accurate estimation, whilst the uncertainties connected with the conditions regulating its sensibility rendered exact comparisons of small differences between different sets of experiments impossible. We therefore used the galvanometer in all the remaining experiments, obtaining with it results which could be better relied upon for purposes of comparison.

Section 5.—Electrical Changes Produced by Localised Stimulation of the Columns of the Cord.

Plan of Experiments.

In order to obtain quantitative comparisons between the effects evoked by localised excitation of different columns in the cord, the plan adopted was to divide the cord in the mid-dorsal and lumbar regions, and prepare one end of the isolated experimental tract lying between the sections for connection with the galvanometer electrodes and the other for excitation. The method of connection has been already fully described, namely, at the cross section and the surface 1 centim. away, by means of cables, under all precautions previously indicated. The preparation of the other end for excitation was effected by removing about a centimetre from the end, and thus exposing the cross section of the cord, in which it was possible, using the precautions described in the chapter on operative procedure, to stimulate, with a pair of fine platinum electrodes, the section of each column thus exposed, anterior, lateral, posterior, or the grey matter.

The experiments showed us that with moderate intensities of stimulating currents, electrical effects were always produced in the observed end of the experimental tract, when at the other end the cross section of either lateral or posterior column was excited, but that only very small and rare effects were caused by a similar excitation of the anterior columns or of the grey matter. This suggested that no continuous strand of fibres united the excited portion of these latter tracts with the observed portion. We shall refer to this result again later on ; since, however, the stimulation of the lateral and posterior columns alone gave notable effects, we limited our excitation in the majority of instances to these columns.

The majority of these experiments were carried out on Cats (17 animals), but we also made a considerable number of experiments on three large Macaque Monkeys. It will be presently seen that the results differ in the two animals in a most interesting way.

The experiments all fall into two great groups, distinguished by the fact that in one the lumbar end of the isolated fragment of cord was the seat of galvanometric observation, whilst, in the other, the dorsal end was observed and the lumbar end excited. In the first case the electrical changes are obviously due to the discharge of nerve impulses *down* the cord, in the second to their discharge *up* the cord.

We will now proceed to a detailed description, first of a typical experiment, and then of the results obtained from several experiments under these two opposite conditions, and we will take first the case of impulses descending the cord, these impulses having been produced by excitation of some one column, as displayed in the dorsal section of the "experimental region" of cord. The galvanometric connections having been made with the lower lumbar end of this tract, electrical changes were evidenced in it when the descending impulses reached that part which was in connection with the electrodes leading to the instrument.

Section 6.—Electrical Effects evoked in the Lumbar Cord by Excitation of the Columns in the Dorsal Region.

(*a.*) *Typical Experiments.*

Since the results in the case of Cat's cord, as mentioned in the preceding paragraph, are different from those obtained with the Monkey's cord, it is desirable to separate out the experiments made upon each. We will therefore describe a single typical experiment and its results in the case of these animals. In order to avoid repetition, the general procedure, which is the same in both animals, will be described more minutely in the case of the Cat (this being taken first) than in that of the Monkey. To make clear the relationship of the excitation to the galvanometric connections, the actual positions in a typical case of the seat of operation and of both sets of electrodes is given in fig. 10, p. 368, which represents the spinal cord of an animal thus experimented upon.

The cord of the Cat (243) was divided at the level of the 7th dorsal vertebra; it was then exposed in the lumbar region for 3 centims. and divided at the level of the 3rd lumbar vertebra, thus isolating an experimental region which extended between these two levels. The distal (lumbar) end of this isolated fragment was now ligatured, and all connections having been divided, was raised in air by the thread. By means of cables the transverse section was connected with one non-polarisable electrode, the longitudinal surface at 1 centim. distance by a similar cable with the other. The electrodes were fixed, as before, on a stand, and arranged at such a height that a considerable length, two or three inches, of thread cable hung loosely between them and the cord, all error due to mechanical displacement, as in the cortical experiments, being thus guarded against. The upper end of the isolated fragment or experimental

tract of cord was now exposed for about a centimetre, and a fresh division made so as to expose a more excitable section for stimulation.

The portion of cord investigated showed, when connected with the galvanometer, the usual resting electrical difference between the surface and ligatured cut end (see Chapter IV.).

When after compensation the galvanometer needle was steady, the exciting electrodes, guarded by a short-circuiting key, were carefully held by one observer against the cut end of one column of the cord, as described in Chapter III., every precaution being taken to ensure that the surface should be dry. The key was now opened by the observer at the galvanometer, and by means of the revolving paraffin key the column was stimulated for a definite time ($3\frac{1}{2}$ seconds in this case), by a series of weak induction currents (100 per second) produced by the usual magnetic interruptor, and made equal and alternate by means of the Helmholtz side-wire. The intensity of the exciting currents had to be adapted to the varying condition of the animal, etherisation, &c., but the results aimed at being to stimulate the fibres in the separate columns rather than to arouse the reflex activity of the cord, it was thought advisable, at any rate in the commencement of an experiment, to use currents only just sufficient to evoke definite effects; such excitation will be termed here "minimal."

In this particular case one Daniell cell was used in the primary exciting circuit and the secondary coil stood at 500. The excitation of either anterior column produced no electrical change; that of either lateral produced a very distinct effect, of the usual excitatory character, that is, an effect which commenced with the stimulation and did not persist after its cessation.

The effect indicated the establishment of a transient electrical state, opposed in direction to that of the original resting difference. The galvanometer deflection, which recorded the change, was very distinct in its commencement and termination, so that its amount could be determined with accuracy. The deflection was 41 when the left, and 57 when the right lateral column was excited. The stimulation, in exactly the same way, of the cut end of the posterior columns produced much more pronounced effects, amounting to 96 in the case of the left, and 94 in that of the right column. Every precaution was taken to ensure that as far as possible the degree of narcosis, &c., should be the same during the four stimulations, and an interval of 1 minute was generally allowed to elapse between the successive applications of each.

When a stronger stimulus (double the strength, coil 1000), of precisely the same character and duration was employed, larger effects of the same kind were produced, stimulation of the anterior regions being again followed by only a mere trace of effect, that of either lateral by well-marked deflections (left 105, right 140); and that of the posteriors by very large deflections (left 290, right 208).

It will be seen that this relationship of magnitude of effect is one which is retained in all the results obtained in this way by differential columnar excitation of the divided cord of the Cat.

A very different relationship is, however, found to exist when the spinal cord of the Monkey is investigated in a similar way.

The spinal cord of a Macaque Monkey (232) was divided at the 10th dorsal vertebra for excitation, and also at the 2nd lumbar, where having been freed from its nervous

Fig. 12.

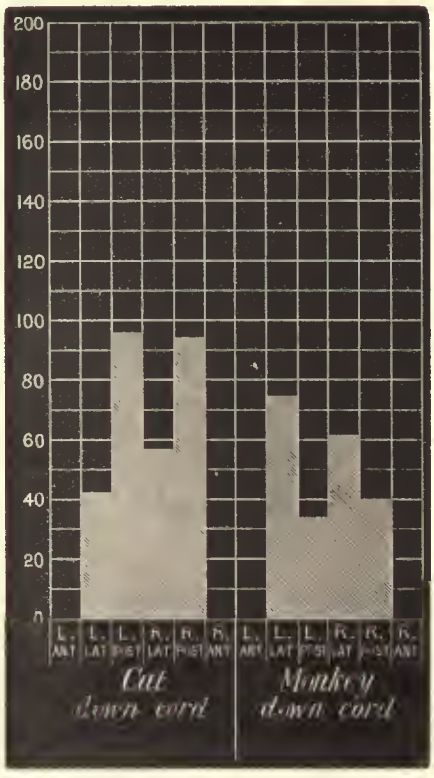
and other attachments, it was ligatured near its divided end, raised as in the preceding experiment, and by means of cables connected with the leading off non-polarisable electrodes at its ligatured end and at its surface (see fig. 12).

The usual resting electrical difference was observed when the electrodes were connected with the galvanometer, and was compensated. Each column was now

excited where it had been exposed in the dorsal cross section, the excitation being as in the preceding case, viz., that of the interrupted induction currents (100 per second) with the Helmholtz side-wire, and the period of excitation being $3\frac{1}{2}$ seconds.

As in the Cat, the excitation of either anterior column produced no effect; that of each lateral, however, evoked a marked electrical effect, the two laterals giving respectively, left 75 and right 62, the deflection being in each case opposed in direction to that of the resting difference. Excitation of either posterior column was followed by a much smaller deflection than the corresponding lateral, the left giving 34, the right 40.

Fig 13



When a stimulus of double the strength (coil 1000) but of the same duration was employed, very large deflections were produced, but the relationship of the results still held good, as excitation of the left lateral gave 210, whilst that of the corresponding posterior gave 165, and similarly excitation of the right lateral gave 140, whilst that of the corresponding posterior gave 120.

If the comparative value of the electrical change produced in the cord by "minimal" excitation of the different columns be represented graphically, as in the annexed figure, a glance is sufficient to show the striking contrast between the result obtained in the Cat and that obtained in the Monkey, since in the latter case the laterals predominate over the posteriors. (See fig. 13.)

(*b.*) *Average of Experiments.*

The two experiments just described are types of all those made upon normal animals. The following table gives the results of the readings obtained in four Cats and one Monkey, with stimuli which were varied in one particular only, that of intensity.

It will be noticed that the average in the Cat of the deflections produced by excitation of the posterior columns is twice as great as that following stimulation of the laterals.

In the Monkey, on the other hand, the average of the stimulation effects obtained from the lateral is about half as large again as that produced by the excitation of the posterior columns.

EXCITATION of Cut Dorsal Cord (Peripheral Surface). Electrical Effect in Lumbar Cord.

	Region observed.	Region excited.	Intensity of stimulus.	Electrical effects evoked by stimulation of					
				Left.			Right.		
				Ant.	Lat.	Post.	Ant.	Lat.	Post.
Cat (243) . .	2 Lumbar	8 D.	500 min.	trace	41	96	trace	57	94
,, ,, .	,,	,,	1000 max.	,,	105	290	,,	140	208
,, (351) . .	1 ,,	7 D.	250 min.	..	33	70	..	55	62
,, ,, . .	,,	,,	,,	..	12	39	..	42	52
,, ,, . .	,,	,,	500 max.	..	90	170	..	..	..
,, ,, . .	,,	,,	,,	..	31	70	..	90	105
,, ,, . .	,,	,,	,,	..	56	110	..	91	115
,, (230) . .	13 Dorsal	10 D.	500 min.	..	30	130	..	65	150
,, (378) . .	3 Lumbar	,,	,,	..	48	86	..	41	123
,, ,, . .	,,	,,	,,	..	48	92	..	32	105
,, ,, . .	,,	,,	1000 max.	..	39	225	..	62	197
,, ,, . .	,,	,,	,,	..	75	175	..	98	207
					608	1553	..	773	1418
			General	average	51	129	..	70	129
Monkey (232) .	2 Lumbar	10 D.	500	..	75	34	..	62	40
,, ,, .	,,	,,	,,	..	98	22	..	65	30
,, ,, .	,,	,,	1000	..	210	165	..	140	120
			General	average	128	74	..	89	63

A further result which an analysis of these effects shows, is the difference between the average deflection in the case of the posterior and the lateral column with weak minimal stimulation and maximal stimulation respectively.

AVERAGE effect evoked by stimulation of one lateral column.

	Cat.	Monkey.
Minimal stimulation . . .	42	75
Maximal „ . . .	87	175

AVERAGE effect evoked by stimulation of one posterior column.

	Cat.	Monkey.
Minimal stimulation . . .	92	31
Maximal „ . . .	170	142

It is seen that in the Cat both minimal and maximal stimulation evoke effects which are twice as large in the case of the posterior columns as in that of the laterals.

In the Monkey the lateral column effect with minimal stimulation is, on the other hand, twice as large as that produced by the stimulation of the posterior column, but with a stronger stimulus this relationship does not hold, owing, possibly, to the increased reflex discharge which excitation of the posterior column now evokes.

The difference between the results of excitation of the columns in the two animals is, therefore, best marked with the weaker intensity of stimulus. It is evident that this must depend upon the number of fibres which form direct connections between the excited dorsal and observed lumbar region, along which fibres as constituting paths of least resistance the nerve impulses are almost entirely propagated from the excited area, when the fibres this contains are aroused by a weak stimulus.

This seems to us to afford an experimental proof of the relatively larger number of continuous lateral column-fibres which must exist in the Monkey as compared with the Cat; this greater proportion may, in the light of the previous results described under cortical stimulation (Chapter V.), be ascribed to the more complete development of the fibres forming the pyramidal tracts.

The histological investigation of the fibres in the tract in the two animals seems to support this view, there being apparently many more fibres in the pyramidal tract of the Monkey than in that of the Dog, as determined by the degeneration method. It is, moreover, to be expected that the fibres in question must increase in number with the completeness of the differentiation of those cortical structures from which

they spring; and it need hardly be pointed out that, whilst minute localisation of representation of movements on the cortex of the Monkey has been clearly demonstrated, such perfect differentiation has not been found in the Carnivora.

We will now pass on to the consideration of the results obtained when the dorsal portion of the experimental tract of the cord is connected with the galvanometer, and the columns excited in the lumbar region, thus evoking impulses which, to produce effects, must pass *up* the cord.

Section 7.—Electrical Excitation Effects evoked in the Dorsal Region of the Cord by Excitation of the Columns in the Lumbar Region.

In these experiments the cord was divided in two places, as described in the preceding paragraphs; but, since the electrical effects in the dorsal end of the tract thus isolated were to be investigated, the cord was prepared for several centimetres at the upper dorsal level. At the lower lumbar section the cord was prepared by excision of one centimetre for purposes of excitation. The exciting and galvanometric arrangements were of the same character as before, their relative disposition being sufficiently indicated in the annexed fig. 14.

(a.) *Typical Experiments.*

We will again first describe the results of an experiment selected as a typical one, and carried out on the spinal cord of the Cat (244), as follows.—

The cord was divided at the 7th dorsal vertebra and prepared for observation as before described: it was then divided at the 2nd lumbar vertebra for excitation.

The upper end of this experimental tract showed the usual resting electrical difference between surface and cross section, which was compensated.

The cut lumbar surface of each different column was now excited for $3\frac{1}{2}$ seconds by the interrupted current, 100 per second (Helmholtz side-wire), and the galvanometric effect observed.

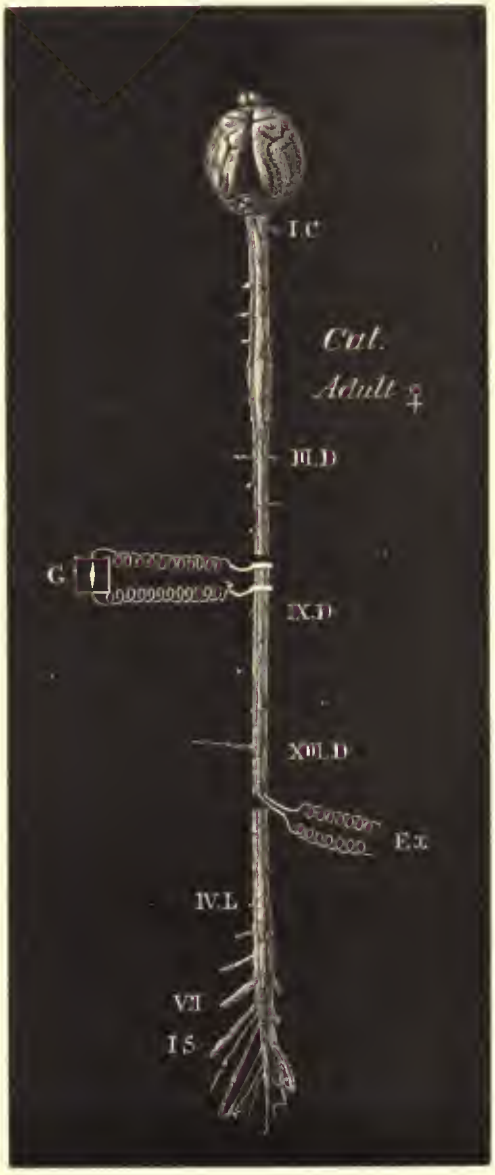
Although the secondary coil stood at only 500, the preparation was very excitable. Excitation of the anterior columns was followed by a slight but distinct effect, 22 with left side, 28 with the right; these, however, did not occur on repetition, and are exceptional.

On exciting the left lateral column, a deflection of 120 was observed, whilst on exciting the left posterior column, a deflection of 215 was produced; finally excitation of the right lateral was followed by 100, of the right posterior, by 190.

The general relationship of magnitude of electrical change evoked in the cord of the Cat by lumbar excitation of the cross sectional area of its different columns is thus the same as that obtained by dorsal excitation.

That is to say, whether the nerve impulses proceed down the cord from an upper excited to a lower observed area, or up from a lower excited to an upper observed area, the anterior column fibres give no effects or only small ones, the lateral give marked effects, but the posterior give still more pronounced effects.

Fig. 14

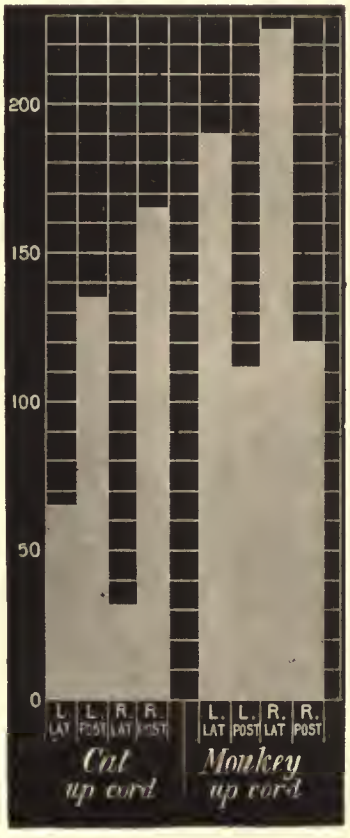


If we turn now to experiments upon the Monkey's cord, the same contrast with the results in the Cat appears as was described before. Thus in a Macaque Monkey (271) the cord was exposed and divided at the 8th dorsal vertebra and was then freed from its attachments, ligatured on the peripheral side of the section and raised

from the canal; it was then connected with the electrodes exactly as in the case of the Cat.

The lower section and exposure occurred at the level of the 1st lumbar, and the cut surface of the columns was then stimulated as in the preceding case. The necessary strength for minimal excitation was only found when the coil was 2000. The anterior columns evoked no definite effect, but excitation of the laterals evoked large effects, left 190, right 225, whilst similar excitation of the posteriors evoked smaller deflections, left 112, and right 120.

Fig. 15.



The results of these two typical experiments will be rendered still more obvious by the annexed figure, in which the value of the excitatory effects in the Cat and Monkey are displayed in a graphic form. It will be seen how completely the relative size of the effect evoked by stimulation of the two kinds of column is reversed in the two animals. (See fig. 15.)

(b.) *Average of Experiments.*

We will now take the average of the observations in which the condition of the animal, &c., was, as far as possible, the same throughout, and the effect evoked in the dorsal cord by stimulating the lumbar columns accurately noted.

Excitation of Cut Lumbar Cord (Central Surface). Electrical Effect in Dorsal Cord.

	Region observed.	Region excited.	Intensity of stimulus.	Electrical effects evoked by stimulation of					
				Left.			Right.		
				Ant.	Lat.	Post.	Ant.	Lat.	Post.
Cat (197) . .	10 dorsal	1 lumbar	2000 max.	0	64	135	0	32	165
Cat (244) . .	8 dorsal	,,	500 ,,	trace	80	120	trace	95	160
,, . .	,,	,,	,, ,,	22	120	215	28	100	190
,, . .	,,	,,	,, ,,	0	126	120	14	66	100
,, . .	,,	,,	,, ,,	..	160	230	..	125	140
Cat (256) . .	8 dorsal	3 lumbar	300 min.	..	65	76	..	20	90
Cat (355) . .	8 dorsal	2 lumbar	1000 max.	..	65	80	..	140	82
,,	,,	,,	,, ,,	..	80	50	..	142	105
,,	,,	,,	,, ,,	..	110	151	..	115	175
Cat (375) . .	9 dorsal	2 lumbar	500	..	145	125	..	145	78
,,	,,	,,	250 min.	..	61	46	..	41	54
,,	,,	,,	500 ,,	..	60	82	..	81	98
,,	,,	,,	1000	..	192	273	..	165	295
,,	,,	,,	1000	..	243	295	.	210	410
,,	,,	,,	500	..	190	140	..	68	215
				..	1761	2138	..	1545	2357
			Average .	..	117	148	..	103	157
Monkey (233)	7 dorsal	1 lumbar	2000	..	..	..	..	120	92
			2000	..	..	..	..	75	20
Monkey (271)	8 ,,	2 ,,	2000	..	190	112	..	225	120
			Average .	..	190	112	..	140	77

It will be noticed that the general relationship holds in the case of impulses passing up the cord, namely, that in the Monkey the most marked effects are evoked by excitation of the lateral, in the Cat by excitation of the posterior columns. There are, however, differences in the precise characters of the relationship as compared with that indicated in the preceding group of observations when the nerve impulses were descending. These differences are exhibited by separating all the lateral and posterior column effects, in accordance as they were obtained with the minimal and maximal stimulation, respectively.

Excitation of Lumbar Cord. Electrical Effect in Dorsal Cord.

Cat.—Average effect evoked in the Cat by stimulation of one lateral column.

Mimimal stimulation	55
Maximal „	124

Average effect evoked in the Cat by stimulation of one posterior column.

Minimal stimulation	74
Maximal „	164

Monkey.—Average effect evoked by stimulation of one lateral column.

Maximal stimulation	133

Average effect evoked by stimulation of one posterior column.

Maximal stimulation	86

The chief differences between these results obtained when nerve impulses proceeded up the cord and those obtained when they travelled down, are the following :—

(1.) The maximal effect in the Cat is more than twice as great as the minimal with stimulation of both lateral and posterior columns when the impulses are ascending, *i.e.*, the lumbar end excited. On the other hand, when the impulses are descending the maximal effect was less than twice as great. There is thus a gain in the amount of the effect, when the stimulus is on the lumbar side of the region, in proportion as the excitation increases in intensity.

(2.) The minimal posterior column effect with ascending impulses is larger than the lateral in the Cat in the proportion of 3 to 2, but this proportion is less than that obtained when the dorsal cord was excited and descending impulses evoked, since this was 2 to 1.

(3.) In the Monkey the lateral column effect is larger than the posterior in the proportion of 3 to 2, when ascending impulses are evoked by maximal stimulation; with descending impulses similarly evoked the proportion is 9 to 7.

The characteristic predominance of the lateral column of the Monkey is however marked, whether the excitation is dorsal and the descending impulses investigated, or lumbar as in the present case, and the ascending effects observed.

The differences above described seem to indicate that the generated impulses travel not only along direct but indirect paths, that is along paths involving cells, and that the structural relations and physiological effects of the interposed structures are such that these influence, in both animals, traversing nerve impulses differently according as their direction is centripetal or centrifugal. It is particularly as regards the lateral column effect that this influence of direction is most marked; it would, therefore, seem that the lateral column comprises among its fibres some (presumably internuncial) which offer less resistance to ascending than to descending impulses. This view will receive confirmation, and be again referred to in the later experiments on the relations of the cord to the nerves. (See Chapters IX. and X.) It is sup-

ported by the series of experiments to be next detailed, in which the result of intervening localised section of columns upon the electrical effects evoked by excitation of the same is set forth.

Section 8.—The Electrical Changes in each half of the Longitudinally Divided Cord.

The question as to what amount of the electrical effects, and thus of the excitatory processes underlying these, when evoked by stimulation of one column, is due to changes confined to that column only, is one of such importance in respect to the well-known views as to conduction by the different groups of fibres in the cord that it seemed advisable to approach this subject by particular experiments. In the case of the changes in the cord following excitation of the cortex, we had found that it was possible to split the cord longitudinally without destroying the excitability of the two halves, and so to obtain evidence of unilateral localisation of effect. This seemed the most straightforward means of getting information as to localisation when the columns of the cord were the seat of the excitation; at the same time we felt that the operation of longitudinal division must in all probability seriously affect the functional continuity of the posterior columns, whose excitation in the Cat, as the foregoing experiments have shown, is productive of such marked results. To these experiments attention must now be given.

We have only performed two successful experiments; both upon the Cat.

In the first the cord was divided at the 9th dorsal and at the 4th lumbar vertebræ. The upper dorsal end of the fragment was prepared for excitation, the lower lumbar end was freed and split in a manner similar to that employed in the cortical experiments. (See fig. 16.) Each half was connected with a pair of non-polarisable electrodes, as in those experiments, and either pair could be switched into the galvanometer circuit and its electrical changes observed. The general arrangement of the circuit in this case is shown in fig. 1.

When the columns were excited for 5 seconds with the secondary coil at 2000, and the right portion of cord investigated, then—

Excitation of the right lateral produced an effect of 31,
„ left „ „ no effect.

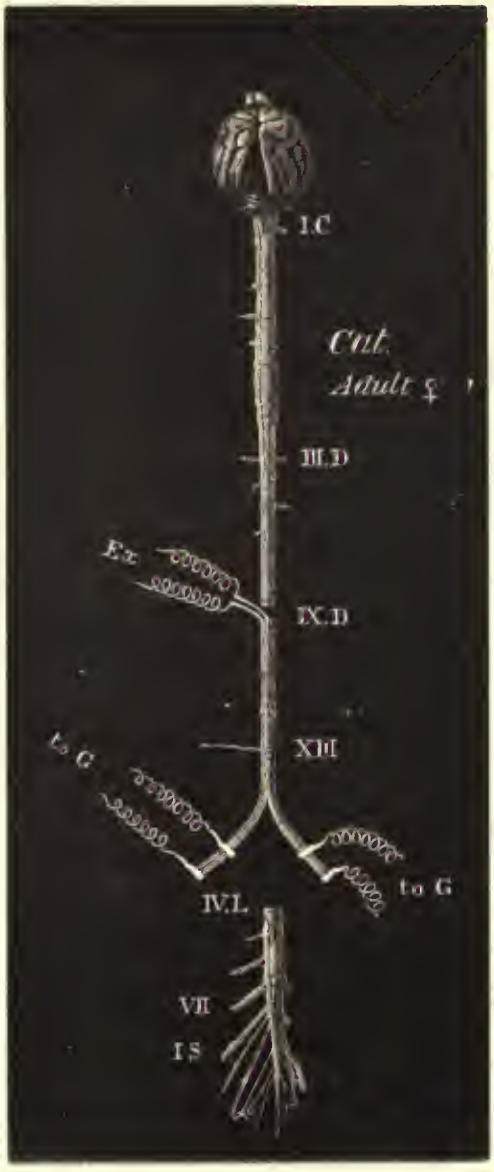
On the other hand,

Excitation of the right posterior produced an effect of 53,
„ „ left „ „ „ 15.

The left portion of cord was now investigated and the same strength of stimulus employed. It was found that—

Excitation of	left lateral	produced	effect of	42 ;	56
,,	right	,,	,,	6	0
,,	left posterior	,,	,,	87	
,,	right	,,	,,	45	

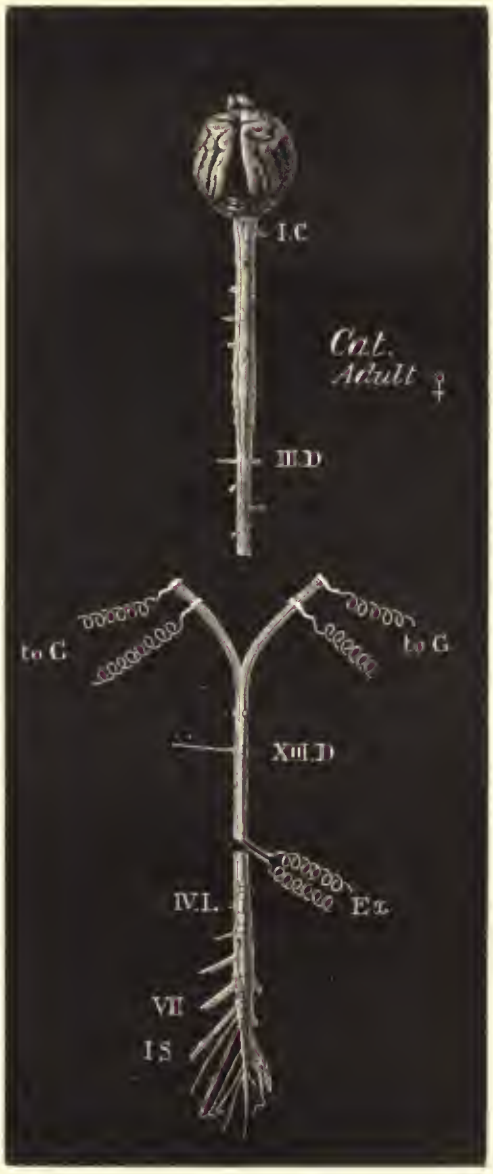
Fig. 16.



On repeating this experiment with a stronger stimulus (coil 3000), the unilateral character of the right lateral column became less marked, whilst the left and right posterior columns gave now equal bilateral results ; thus—

Excitation of left lateral produced effect of 68
„ right „ „ „ 36
„ left posterior „ „ 96
„ right „ „ „ 89

Fig. 17.



It thus appears that when half the split cord is observed and the columns excited on the central side, the excitatory electrical change, produced by weak excitation of the lateral column is entirely confined to the side stimulated, whilst that produced by similar excitation of the posterior column is but mainly confined to the stimulated side, while when the excitation is of sufficient intensity it is produced equally on

both sides. This, therefore, suggests that descending impulses in the lateral column are, to a very large extent, confined to these fibres, but those in the posterior column cross into similarly situated fibres on the opposite half of the cord.

A second experiment of the reverse kind was made on another occasion, the excitation being now in the lumbar region, and the impulses evoked thus being ascending. The cord was divided at the 7th dorsal and 3rd lumbar, and the upper dorsal portion was prepared for galvanometric observation, and split longitudinally, whilst the lower lumbar portion was prepared for excitation; the general arrangement is shown in fig. 17.

When the right half of the split cord was examined—

Excitation of the	right	lateral	produced an effect of	38
,,	left	,,	,,	3
,,	right posterior	,,	,,	40
,,	left	,,	,,	14

The cord was then again divided a little centrally to the seat of the previous excitation, so as to expose a fresh surface for the stimulation, and now—

Excitation of	right	lateral	produced effects of	86 ;	94
,,	left	,,	,,	16	15
,,	right posterior	,,	,,	81	112
,,	left	,,	,,	52	60

The left half of the cord when observed gave the following results:—

Excitation of	left	lateral	produced effect of	33
,,	right	,,	,,	3
,,	left posterior	,,	,,	40
,,	right	,,	,,	7

The general conclusion to be derived from these experiments is that the excitation of the lateral column produces an effect which is limited to a very remarkable degree to the side excited. On the other hand, the excitation of one posterior column produces with appropriate excitation bilateral electrical effects, but the effect is twice as great on the same side as it is on the opposite one.

It must, however, be borne in mind that the operation may, by depressing the excitability of the posterior columns, be a source of error which can interfere largely with the above results, since the posterior columns are more liable than the lateral to suffer by the procedure of splitting, and earlier experiments have convinced us that if they are injured the electrical change produced by their excitation is very largely affected.

The extent to which the effects and thus the nerve impulses are localised in the

columns excited was, therefore, now approached by another method, that, namely, of intervening sections.

Section 9.—Influence of Intervening Sections upon the Electrical Change in the Cord following Excitation of the Different Columns.

The extent to which the electrical change in the cord following excitation of the cut columns is dependent upon direct continuity of nerve fibres between the part of the column excited and the part of the cord observed is more clearly indicated by the experiments now to be described.

In these the excitatory and galvanometric arrangements were similar in all details to those employed in the two preceding groups of experiments; but the experimental tract had been subjected to important additional operations, some particular column indicated being divided at a position intervening between the region of excitation and the observed region, and the result of such division as affecting the electrical excitatory change being then estimated.

The section, the influence of which was thus investigated, was made in most cases at the time of the experiment. In a few cases the section was made three or four weeks beforehand, in order not only to ensure a more striking alteration of effect by the degeneration of the continuous nerve tracts involved, but also to provide against any transient disturbance due to the operation, affecting the excitability both of the particular tract and of other nerve tracts than the one operated upon.

Since the influence of each separate intervening section had to be studied in the case of excitation evoking both descending and ascending impulses in the experimental tract, the experimental results of any section naturally fall into the two groups already indicated in the preceding Sections.

(1.) *Electrical Effects in the Lumbar Cord Evoked by Excitation of the Dorsal Cord.*

A. *Influence of Hemisection.*

The experiments were made upon three animals (Cats), in all of which the intervening hemisection occurred at the level of the 12th dorsal vertebra; in the first on the right side, in the second and third on the left side.

Each experiment was conducted precisely as those previously described; that is to say, the cord was divided at the 8th dorsal and 2nd lumbar vertebræ. The lower end of the experimental tract was prepared for connection with the galvanometric electrodes, the upper for excitation. The different columns were first successively excited before the hemisection in the usual manner, and the electrical effects observed. These are shown in the preceding table, see page 381, and were of the kind indicated in Section 6 (*b*). The cord was now exposed at the 12th dorsal, the hemisection made and the electrical effects of the excitation of the different columns

under these circumstances were then noted. The following is a table showing the results obtained :—

Electrical Effects in Lumbar Cord Evoked by Excitation of Dorsal Cord after Intervening Hemisection on the Right Side at 12th Dorsal Vertebra.

	Region observed.	Region excited.	Stimulus.	Electrical effects.			
				Left.		Right.	
				Lat.	Post.	Lat.	Post.
Cat (351)	2nd lumbar	7th dorsal	500 min.	45	71	0	0
			,, min.	62	45	0	0
			,, min.	43	55	0	0
			1000 max.	100	81	0	0
			2000 max.	201	145	6	26
			2000 max.	180	145	12	31

Intervening Hemisection on Left Side at 12th Dorsal.

	Region observed.	Region excited.	Stimulus.	Electrical effects.			
				Left.		Right.	
				Lat.	Post.	Lat.	Post.
Cat (371)	1st lumbar	8th dorsal	500	18	0	132	56
			,,	18	0	126	75
			,,	15	12	110	58
			1000	49	26	201	193
			,,	29	26	184	182
Cat (278)	3rd lumbar	9th dorsal	500	0	0	47	56
			1000	19	34	148	198

The average results of the excitation of the lateral and posterior columns, when grouped, as dependent upon the intensity of the stimulus, show the following quantitative comparison.

Average Effects obtained by Exciting Columns on Side of Section.

	Minimal stimulation.	Maximal stimulation.
Lateral	8	23
Posterior	2	29

Average Effects obtained by Exciting Columns on Opposite Side to Section.

	Minimal stimulation.	Maximal stimulation.
Lateral	74	183
Posterior	62	173

From this table it will be seen that the electrical effects observed in the dorsal region are profoundly modified by an intervening hemisection of the cord. With an excitation of minimal intensity, the application of the stimulus to the columns at the dorsal end situated on the side of the section evokes little or no electrical effect in the lumbar region. The interruption of the directly continuous fibres by the hemisection has thus reduced the effect to such an extent, that in two Cats it was completely abolished, and only present in one.

With the same minimal intensity of stimulus, excitation of the posterior column evoked no effect at all, except in one instance; the interruption in the fibres of this column thus abolishes the electrical effect.

With a minimal stimulus, therefore, the electrical effect in the lumbar region obtained by excitation of the columns in the dorsal region is dependent upon an unbroken continuity in the fibres descending along the same side as the excited column. It is thus clear, that not only are the stimulating induction currents which traverse the excited end of the exposed column confined to that side of the cord, but, in addition, that the nerve impulses generated by this stimulus travel down that side, since it is the arrival of the nerve impulses at the lumbar end of the tract which produces the electrical effect and this is practically abolished by the interruption offered by the hemisection.

Whilst the experiments thus furnish strong evidence against any direct and continuous tract of nerve fibres passing from one side of the cord to the other, the presence of effects on the two sides of the cord, when evoked by more intense stimuli, shows that the interruption of hemisection is not a complete block. With increasing intensity it will be noticed that excitation of both lateral and posterior columns on the side of section evoke electrical effects in the cord below. These must be due to the passage of nerve impulses from the excited area along paths which are in relation with cells, *i.e.*, indirect, since these are the only known channels across the cord. These impulses may discharge, in a reflex manner, the cellular energy of both sides of the cord, the opposite side in a much less degree than the same side; a crossed electrical change would then indicate the sum of the nerve impulses evoked in the opposite side by a discharge of nerve cells. Similar effects would, however, be obtained if, without any reflex influence being present, an indirect path crossed from the columns of one side to a column of fibres on the opposite side. Both agencies may

be presumed to operate in these cases, though the results of the experimental observations set forth in the succeeding chapters all favour the supposition that the fibres which form the indirect crossed path are almost entirely derived from the posterior column, whilst the internuncial fibres, by which the successive segmental groups of cells are associated with one another, are mainly confined to the lateral column. It will be observed that the *crossed* effect is only $\frac{1}{8}$ to $\frac{1}{6}$ of the direct effect evoked by stimulation of the side opposite to the lesion; hence either the nerve impulses, of which the effect is the index, are either greatly reduced in quantity by their passage through the grey matter, or comparatively few nerve impulses take this crossed path.

Finally, as regards the effects in the side opposite to the lesion, it will be noticed that, comparing the relative value of the two effects, due to excitation of the posterior column is now less than that of the lateral column. This is probably due to the necessary exposure of the columns at the 12th dorsal vertebra acting injuriously upon the excitability and conductivity of the exposed but otherwise uninjured posterior column not included in the section.

A glance at the full details of experiments 351 and 371 will show (see table, Section 6 (*b*)), that the same relation was present in most cases before the hemisection was made; the subject will be referred to in more detail in the next paragraph, which deals with the result of section and injury to the posterior columns.

B. *Influence of Section of Posterior Columns.*

The influence of the section of both posterior columns in the lower dorsal region upon the electrical effect evoked in the lumbar region, and thus upon descending nerve impulses, is shown by the following experiment:—

The cord was divided in a Cat (357) at the 9th dorsal and at the 2nd lumbar vertebræ, it was prepared for excitation at the former region, for attachment to the galvanometric electrodes at the latter. The cord was then also exposed at the 11th dorsal vertebra, and, before any operative lesion, an experiment of the customary kind was made. The excitation, with stimulus 500 of the two laterals, gave deflections of 30 and 65, average, 47; that of the two posteriors gave 130 and 150, average, 140. After division of both posterior columns at the 11th dorsal, similar excitation of the lateral columns evoked effects of 60 and 105, average, 82,* whilst that of either posterior column evoked no effect whatever; unfortunately, the effects evoked by stronger stimuli were not observed.

The interruption, therefore, as regards the posterior columns was complete with this intensity of stimulus, and hence all nerve impulses generated by such "minimal" excitation of either column in the dorsal region are propagated to the lumbar region

* It will be seen that the average effect obtained due to excitation of the lateral columns after section of the posterior columns is increased. A similar exaltation occurs in the experiments detailed in Chapter IX., Section 7, C, where the causation of the phenomenon is discussed.

along fibres which do not pass out of these columns, and a strict localisation of nerve impulses is with this intensity of stimulus possible.

The posterior columns are particularly susceptible to injury, since they are especially exposed to danger of drying, &c., in the preparation of the cord. This circumstance must be always kept in view when experiments involving an intervening exposure of the cord are made. We were much puzzled by the result of two experiments in which, after dividing the cord in the dorsal and lumbar regions, we had exposed a portion of the experimental tract in the intervening part, about the 12th dorsal, for subsequent operative lesion. The following results were obtained :—

	Dorsal cord excited.		Stimulus.	Lumbar cord observed.			
	Observed end.	Excited end.		Left.		Right.	
				Lat.	Post.	Lat.	Post.
Cat (316)	2nd lumbar	8th dorsal	min.	90	31	103	28
			max.	190	91	130	85
			max.	165	65	98	115
Cat (371)	1st lumbar	9th dorsal	min.	145	112	140	124
			min.	132	98	144	104
			max.	170	190	240	182
			max.	280	145	192	195
			max.	142	179	153	205
			min.	62	42	73	30
		General	average . .	153	106	141	117

In these cases therefore all lateral column effects average with minimal stimulus 111, with maximal 166 ; whilst all posterior column effects average with minimal stimulus 70, with maximal 145. It is seen that these results are exceptions to the general rule (see p. 385) of the effect from the posterior being in the Cat larger than that from the lateral. That this was really due to the prolonged exposure at the 12th dorsal injuriously affecting the posterior columns is shown by the fact that such exceptional results were only obtained when an intervening portion had been thus exposed. If prolonged exposure is avoided by performing the necessary operation immediately before the desired intervening lesions are to be made no such lowering of the amount of the posterior column effect is observed. In this relation it is possible to explain the comparatively small posterior column effect (see p. 385) of the Monkey as in some measure due to a loss of excitability in these columns, which seem to be much more susceptible than the laterals (CHAUVEAU).

Influence of Section of one Posterior Column.—It is possible to interrupt one column only, and thus to obtain conclusive evidence of the extent to which the

electrical effects evoked by its stimulation are due to the propagation of impulses along fibres which are confined to the column.

This lesion was effected in three Cats on the left side, the results are seen in the following table :—

ELECTRICAL Effect obtained in the Lumbar Cord by Excitation of Columns in the Dorsal Region after intervening Section of Left Posterior Column.

			Stimulus.	Left.		Right.	
				Lat.	Post.	Lat.	Post.
Cat (357)	2nd lumbar	10th dorsal	500 min.	68	12	82	48
			,, min.	75	14	120	70
Cat (371)	1st lumbar	9th dorsal	250 min.	86	0	89	34
			500 min.	115	0	145	66
			1000 max.	198	45	180	170
			,, max.	169	26	146	130
Cat (378)			500 min.	59	3	75	26
			1000 max.	144	34	131	193

AVERAGE Effect obtained from Side of Section.

	Minimal stimulation.	Maximal stimulation.
Lateral	80	170
Posterior	6	35

AVERAGE of Effect obtained from Side Opposite Section.

	Minimal stimulation.	Maximal stimulation.
Lateral	102	152
Posterior	51	164

It will be noticed that with minimal stimulation the interruption occasioned by the unilateral section is almost complete ; hence we conclude that—

(*a.*) The stimulation must be localised to the column on which the electrodes are placed ;

(*b.*) The electrical effect in the lumbar cord, following excitation of one posterior column, must be due to nerve impulses proceeding down channels confined to that column ;

(*c.*) No tract of fibres in other columns can have direct and continuous connections with the fibres in one posterior column.

With maximal intensity of stimulation the interruption is sufficient to lower the posterior effect in the proportion of 164 (that of the uninjured posterior) to 35, that is, 80 per cent. The effect still obtained, in spite of the interruption, must be due to indirect paths which come into relation with cells; these paths may partly cross or be continuous with fibres contained in the uninterrupted lateral columns on the side of the lesion. The next experiment to be detailed (C) will throw some light upon this point.

C. *Influence of Section of both Posterior Columns and one Lateral.*

By making a hemisection and then dividing the remaining posterior column, a lesion is made (MIESCHER) in which the only intact fibres in the cord are those of one lateral column, one anterior column, and the fibres in one half of the grey matter.

Such a lesion was made in two animals at the 12th dorsal vertebra, with the following result on the electrical changes in the lumbar cord.

HEMISECTION on the right side and section of the left posterior column.

	Cord observed.	Cord excited.	Stimulus.	Left.		Right.	
				Lat.	Post.	Lat.	Post.
Cat (357) . .	2nd lumbar	9th dorsal	500 min.	90	0	0	0
			,,	75	0	0	0
Cat (351) . .	3rd lumbar	7th dorsal	2000 max.	140	32	11	16
				135			
				125			

It will be seen that with a "minimal" stimulus no electrical effect was evoked except by excitation of that lateral column (left) which remained intact. Hence, the lateral column minimal effect is as strictly localised to its contained fibres as that of the posterior column, and the presumption is that it contains no fibres which are directly continuous with those which form at the level of the 9th dorsal the other lateral and the two posterior columns.

On the other hand, with a maximal stimulus, excitation of each column evokes an effect, which is, however, much less pronounced than that obtained by the excitation of the uninterrupted lateral. It will be noticed that the posterior column on the side of the uninterrupted lateral gives far the most marked of these effects. If the effects are taken to mean that there exist indirect channels by which nerve impulses may pass from the fibres of any excited interrupted column into those of the uninter-

rupted lateral, then the preponderance of the effect evoked by the left posterior column would show that such indirect communication between the fibres in the posterior column and those in the lateral consists chiefly of posterior column fibres, which do not cross the cord. It may indeed be doubted whether the small effects evoked by excitation of the lateral and posterior columns of the side opposite the uninterrupted lateral are any evidence of veritable crossing nerve impulses, since it is probable, that with the strength of stimulus used (2000), the excitation of any column may cause reflex discharges from the cells in the grey matter of the upper dorsal portion of the cord, and the effect transmitted by the uninterrupted lateral would therefore be due to spread of the awakened activity involving the cells which are connected with its own internuncial fibres, and which thus send forth nerve impulses to be transmitted down the uninterrupted channels.

However this may be, there is no indication by this electrical method of any large indirect crossed path, in connection with the lateral column, of fibres such as would conduct nerve impulses downwards from the dorsal to the lumbar cord. The interest which attaches to this negative result hangs upon the presumed connection of the lateral* tract with nerve fibres on both sides, and upon the circumstance that it forms the first of a series of results all pointing conclusively in the same direction, which will be set forth in Chapters IX. and X.

(2.) *Electrical Effects Evoked in the Dorsal Cord by Excitation of the Lumbar Cord, after intervening Sections.*

A. *Influence of Hemisection.*

Since the characters of the normal electrical effects in the cord are not the same when the nerve impulses are ascending, *i.e.*, evoked by excitation of the lumbar region, as when descending, *i.e.*, evoked by excitation of the dorsal region, it is not surprising that the influence of intervening lesions upon the former group of effects should differ from the influence already described upon the latter group.

The influence of hemisection upon ascending changes was studied in two animals (Cats), one with minimal, the other with maximal stimuli, the experimental tract being situated as shown in the following table, and the hemisection made on the left side at the level of the 13th dorsal and 10th–11th dorsal vertebræ respectively.

* Miescher, 'Arbeiten aus dem Physiologischen Institut in Leipzig,' von C. Ludwig; Woroschiloff, *ibid.*

Intervening Hemisection on the Left Side.

	Cord cut for observation.	Cord cut for excitation.	Stimulus.	Left.		Right.	
				Lat.	Post.	Lat.	Post.
Cat (375)	8th dorsal	2nd lumbar	500	8	0	80	40
Cat (355)	„	„	1000	0	65	105	80
				0	26	106	86
				0	40	120	96

"*Minimal*" *Stimulation.*—In the first Cat (375) the "minimal" stimulation in the lumbar region of the lateral and posterior columns on the side of the section evoked no appreciable effect in the dorsal region, the negative result thus confirming our previous conclusion, that the direct fibres in these columns are completely confined to one side of the cord. This, it may be pointed out, is strictly in accordance with the present state of minute anatomical knowledge, as obtained by the study of the degeneration and developmental histological changes.

Average of Effects with Maximal Stimulation.—With the maximal stimulus, no effect was evoked by the stimulation of the lateral column on the side of the interruption. This contrasts with the fact that when the nerve impulses are propagated down the cord, as in the previously described experiments, such stimulation evoked appreciable effects.

The remaining columns gave average effects of

44 for the posterior column on the side of the section,
110 „ lateral „ „ opposite to the section,
87 „ posterior on the opposite side.

The posterior column thus contains indirect fibres which come into relation with cells, but through these with fibres in the column on the opposite side of the cord, and this connection is such, that apparently it offers less resistance to the passage of ascending or afferent impulses than it does to that of descending ones, or possibly special facilities exist for the discharge of cells in response to impulses ascending in the posterior column.

B. *Influence of Section of Posterior Columns.*

The influence of the section of both posterior columns upon the effect evoked by excitation of the lumbar cord was studied in the case of such lesions made upon three animals (Cats), in two of which the section was carried out at the time of experiment at the level of the 12th dorsal, whilst in the third it was done 28 days before at the level of the 10th dorsal vertebra. The results are displayed in the following table :—

SECTION of both Posterior Columns.

	Cord cut for observation.	Cord cut for excitation.	Stimulus.	Left.		Right.	
				Lat.	Post.	Lat.	Post.
Cat (256)	8th dorsal	3rd lumbar	300	30	0	45	15
			1000 max.	240	65	310	105
Cat (197)	11th dorsal	4th lumbar	2000	64	35	32	25

PREVIOUS Operation, Division of both Posterior Columns.

	Cord cut for observation.	Cord cut for excitation.	Stimulus.	Left.		Right.	
				Lat.	Post.	Lat.	Post.
Cat (251)*	6th dorsal	2nd lumbar	1000	68	0	30	10
			min.	58	2	100	0
			max. (less ether)	80	20	96	28

The differences between the results obtained from sections made at the time and beforehand, are perhaps those involved by the necessity in the latter case of using a slightly stronger stimulus. And since the different column effects are similar in both cases, the massed average of both lateral and both posterior effects evoked with the minimal and maximal stimulus respectively may be taken from all three animals.

Effect evoked by lateral columns.

Minimal excitation, 55; maximal excitation, 136.

Effect evoked by posterior columns.

Minimal excitation, 4; maximal excitation, 46.

It will be seen on looking at these averages, that with minimal excitation the posterior column effect practically disappears as the consequence of the interruption produced by the section; thus the view as to the localisation of both stimulus and generated impulse to these columns is true of afferent as of efferent impulses, when the former is sufficiently weak.

With a relatively more intense stimulus (or with the animal less etherised), this localisation of the effect does not occur; the excitation of the lower and posterior columns now evokes effects above the interruption, the average amount of which is as much as one-third that produced by the stimulation of the laterals, that is to say,

* For full description of this animal as regards its condition during life and the *post mortem* appearances of the cord, see p. 439.

there are indirect fibres in the posterior columns which are not interrupted, and which connect these through cells with the lateral columns. This we have already seen in the case of the lateral column exclusion experiment (see p. 398), to be also true for efferent impulses, hence each posterior column is indirectly connected with the lateral of its own side.

We now pass to the experiments made in similar preparations on one posterior column only.

Influence of Section of one Posterior Column.—Our experiments upon this point were made on two animals, but in each case with a strength of stimulus which was not minimal, since, although in one animal the absolute intensity of the exciting currents was that generally used for minimal stimulation (500), yet the preparation was in a hyper-excitable state owing apparently to the lumbar section having hit the entrance of a posterior root. That the preparation (Cat 375) was hyperexcitable at the moment when the intervening section was to be made, is shown by the fact that with this weak intensity of stimulus the excitation of the lateral columns gave deflections of 166 and 285, and that of the posteriors of 168 and 202. We endeavoured to lower the excitability by more profound etherisation, but the results evidently belong to that class which have been considered as evoked by maximal stimuli. The true effect of minimal excitation was not, therefore, observed. The left posterior column was divided in both animals at the level of the 11th dorsal vertebra.

Electrical Effect obtained in the Dorsal Cord by Excitation of Columns in the Lumbar Region after intervening Section of the Left Posterior Column.

	Cord cut for observation at	Cord cut for exeitation at	Stimulus.	Left.		Right.	
				Lat.	Post.	Lat.	Post.
Cat (375) .	9th dorsal	2nd lumbar	500 max.	108	26	115	58
Cat (197) .	11th dorsal	4th lumbar	2000 max.	70	48	20	205

Average effeet evoked by excitation of the—

(1) Lateral columns 78
(2) Posterior columns on side of lesion 37
(3) Posterior columns on side opposite lesion 131

The interruption in the left posterior column thus did not abolish, but only reduced, the electrical effect present in the dorsal cord above the interruption, when the column was maximally stimulated below in the lumbar region. The amount of the reduced effect is one quarter of that which can be evoked by maximal stimulation of the opposite uninterrupted posterior column. The existence of even a reduced effect is

presumably due to nerve impulses proceeding up channels which are composed of fibres starting below the section in the posterior column, but brought, by the intervention of cells, into relation with fibres contained in the lateral column of the same side, and in the posterior of the opposite side.

An instructive experiment bearing upon this subject remains to be detailed. We divided the posterior roots of the 5th, 6th, 7th lumbar, and 1st and 2nd sacral nerves on the left side. After twenty-one days the animal (Cat 227)* was used for experiments on the cord. These were of the same kind as the previous ones, the cord being divided in the dorsal and lumbar regions, and the experimental tract prepared for attachment to the galvanometric electrodes at its dorsal end and for stimulation at its lumbar. The excitatory electrical effects obtained with excitation of the different columns are given in the following table.

Division of Left Posterior Roots of Sciatic Nerve.

	Cord cut for observation at	Cord cut for excitation at	Stimulus.	Left.		Right.	
				Lat.	Post.	Lat.	Post.
Cat (227) . .	10th dorsal	3rd lumbar	1000	82 125	66 71 41 30	71 145	105 205 61 85

Average effect obtained by exciting both lateral columns 106
Average effect obtained by exciting posterior column on side of lesion 52
Average effect obtained by exciting posterior column on opposite side to lesion 114

It is clear, therefore, that the result of the division of the root was to reduce the posterior column effect on the side of the lesion, the diminution of effect amounting to about a third of what must be considered its full value, since the posterior column effect on the side opposite the lesion is probably lower than it would be in the normal animal.

If, therefore, the stimulus had been of sufficient intensity to evoke impulses transmitted by direct fibres only, then this diminution would mean that a third of these direct fibres had degenerated in consequence of the section. The stimulus, however, was evidently too strong to be classed as "minimal," and all the effects must be considered as increased by the accession of impulses proceeding up indirect paths. Hence, the experimental results suggest that from the total number of direct and indirect fibres uniting the lumbar region of the left posterior column with the dorsal

* For full description of this animal see p. 466.

region, the section of the posterior roots has withdrawn from active service a proportion equivalent to about one-third, and rendered them incapable of conducting impulses.

It is conceivable that the cells in the posterior horn, which, in some animals,* are in relation with the posterior root fibres, may have their functional activity impaired by the section and consequent degenerative changes, and that a small part of the diminution may be due to the withdrawal of impulses possibly generated in them. (See Chapter XI.)

C. *Influence of Section of both Posterior Columns and one Lateral.*

In order to ascertain to what extent ascending impulses started by lumbar excitation of the lateral column are interrupted by its section, a similar experiment to that described with descending impulses was carried out. An intervening hemisection on the left side and a further division of the posterior column on the right side were made; there remained only the lateral of one side, the contiguous grey matter, and the anterior columns to bridge across the interruption (MIESCHER).

The cord was prepared and excited as in all the previous experiments, two strengths of stimulus being used, both more than "minimal."

	Cord cut for observation at	Cord cut for excitation at	Stimulus.	Left.		Right.	
				Lat.	Post.	Lat.	Post.
Cat (355)	8th dorsal	2nd lumbar	1000	0	0	110	19
			2000	0	19	220	40

It is evident from this experiment that (1) the excitation of the uninterrupted lateral column of the right side alone produces a marked effect; (2) that the excitation of the posterior columns can evoke effects in spite of the interruption in the lateral; (3) that effects can be obtained from the posterior column of the same side with an intensity of stimulus which is not effectual in the case of that of the opposite side; (4) that even with the strongest intensity of stimulus used, excitation of the interrupted left lateral column evokes no result. We may, therefore, infer that afferent tracts in the cord lying in one lateral column are brought into relation with the posterior but not lateral column of the other side. The importance of this result will be realised if it be remembered that it has been concluded from the result of physiological experiments (WOROSCHILOFF, &c.), to be detailed in the next chapter (p. 419), that the majority of sensory fibres entering the cord pass into the lateral column of the opposite side, the remainder continuing in the lateral column of the side on which

* See FREUD's paper on the cells in *Petromyzon*.

they enter. It has been shown by the present experiments that, as far as the nerve impulses aroused by electrical excitation of nerve fibres in the cord are concerned, no such extensive crossing occurs in the dorsal or lumbar regions; and the experiments in Chapters IX. and X., on the relation of the cord to the lumbar nerves, show that no such extensive crossing into the opposite lateral column occurs when the impulses are generated in the entering nerves themselves.

It is difficult to perform a satisfactory experiment on the influence of section of one lateral column, since the extensive lesion alters the excitability of the posterior column of the same side, and this interferes with the sharpness of the results. To avoid this we made the experiment upon an animal (Cat 259)* in which thirty-four days previously the lateral column had been severed on the left side at the level of the 10th dorsal vertebra. The cord was then divided and prepared in the dorsal and lumbar regions, and the following results obtained :—

	Cord cut for observation at	Cord cut for excitation at	Stimulus.	Left.		Right.	
				Lat.	Post.	Lat.	Post.
Cat (259)	4th dorsal	1st lumbar	1000	0 Trace	40 50	38 37	40 73

Average of lateral on side of section . . . . . Trace,
Average of lateral opposite to section 37,
Average of posterior columns . . . . . 51.

The lateral column interruption with this intensity of stimulus, which from the inexcitable condition of the cord was practically minimal, is thus sufficient to absolutely block any transmission upwards of nerve impulses generated in those fibres of that column which lie below in the excited lumbar region.

* In this animal, just before the experiment, it was found that there was spastic paralysis in the left hind limb with diminished sensibility. The knee jerks were equal and normally present. On microscopical examination the lesion was found to have destroyed the lateral column of the left side, the outer portion of the anterior column, and the dorsal two-fifths of the posterior column; while, on the right side, a portion of the posterior median was injured. Of descending degeneration there was noted the posterior third of the left lateral and the median portion of the left anterior column. Of ascending degeneration a section at the 5th dorsal showed degeneration in both postero-median columns, extensive on the left side, but only few fibres in the centre of the right column. Left cerebellar and antero-lateral tracts degenerated.

Section 10.—Summary of Results.

It will be well now to express the general conclusions founded upon a comparison of all these experiments, especially those involving the influence of intervening sections upon the cord electrical effects.

I. If a portion of cord be severed by a dorsal and lumbar section from its connections above and below, then stimulation of either lateral or posterior column at one end evokes electrical effects at the other, which are dependent for their amount on the uninterrupted structural continuity of fibres in the particular column excited; and the electrical changes are thus the index of the arrival at one end, of nerve impulses generated at the other, and propagated mainly along the fibres in each column.

II. If the stimulus used be minimal, then the interruption due to the section is in every case sufficient to practically abolish the effect; hence, with this stimulus, the nerve impulses aroused by localized stimulation of fibres, which are exposed in the section, are entirely confined to the particular column excited. This is true, whether the stimulus be central or peripheral to the observed region, that is, whether the impulses are ascending or descending.

III. If the stimulus be maximal, then a greatly reduced effect is still obtained, in spite of the interruption. This effect is due to nerve impulses, which must at some period be conducted along indirect fibres outside the excited column. Its average amount varies in the different columns. These amounts may be arranged in series as shown in the following table, in which the nature of the excitation and of the interruption is noted, and the average effect evoked by maximal stimulation is given.

Character of impulses.	Column excited.	Column interrupted.	Effect.
Ascending	Lumbar end of cut posterior	Section of same posterior	52
		Section of both posteriors	46
		Hemisection same side	44
		Section of both posteriors and lateral of opposite side	40
Descending	Dorsal end of cut posterior	Section of same posterior	35
		Section of both posteriors and opposite lateral	32
		Hemisection same side	29
	Dorsal end of cut lateral	Hemisection same side	23
Ascending	Lumbar end of cut posterior	Section of both posteriors and lateral of same side	19
Descending	Dorsal end of cut posterior	Ditto	16
	Dorsal end of cut lateral	Section of both posteriors and lateral of same side	11
Ascending	Lumbar end of cut lateral	Hemisection same side	0
		Hemisection same side and section of posterior of opposite side	0
		Section of lateral same side	0

IV. The table just given indicates that the indirect path along which impulses are conducted from the excited end is not confined to the column, and suggests that the size of the effect evoked indicates the amount of indirect connection through cells with other columns.

V. The magnitude of the indirect effect evoked is greatest in the case of the lumbar excitation of the posterior columns; the afferent indirect connections leading upwards from this column are, therefore, either very numerous or offer little resistance, and spread largely into other regions.

VI. The effect is still comparatively large when evoked by dorsal excitation of the interrupted posterior column. There are, therefore, indirect connections leading downwards towards the periphery, possibly the same to some extent as those just mentioned in V., but either less numerous or offering more resistance, or spreading to a less extent into other regions.

VII. The excitation of the dorsal end of the interrupted lateral column evokes electrical effects, hence indirect connections are thereby suggested spreading from the lateral column downwards into other regions; these, however, are less numerous or offer more resistance than those mentioned in VI.

VIII. The excitation of the lumbar end of the interrupted lateral column evokes no effect, hence all the channels in this column, by which impulses could pass upwards, are absolutely confined to the column.

IX. The striking feature of the preceding conclusions is that the connections of the fibres of the posterior columns are framed on a different plan from those of the laterals. The posterior column fibres spread into other columns both as they ascend and to a less degree as they descend; the lateral fibres, however, spread into other columns particularly as they descend. The posterior columns offer thus special facilities for conveyance and distribution of afferent impulses; the lateral special facilities for the conveyance and distribution of efferent impulses.

It will be remarked that the conclusions just suggested as to the relations of the columns are in accordance with the views of Schiff, "die Hinterstränge bis ins Hirn hinein bilden die Legislative, die Türck'schen Bündel erwecken die Exekutive."

In conclusion, we draw attention to the general indications as to the structure of the cord which the whole of these experiments imply.

Since the electrical effect obtained by the "minimal" stimulation of the cut end of one column is apparently due to the excitation of the direct fibres in that column only, the average amounts obtained in the case of the different columns is related to the excitability and number of the fibres contained. As regards the excitability of the direct fibres in different columns, there is no reason for supposing that these direct fibres, which have no connection with cells between the two ends of the experimental tract, are in any marked degree more excitable in one column than in another. The amount of the "minimal" effect must therefore depend upon the number of fibres

excited, and a comparison of the amounts in the two columns would thus give a rough estimate of their comparative number.

In the Cat the effects up and down evoked by the minimal excitation of the posterior column are 92 and 74, that is an average of 83 ; those similarly evoked by minimal excitation of the lateral column are 42 and 55, giving an average of 48. Hence we infer that the direct fibres in the Cat between the dorsal and lumbar regions are nearly twice as numerous in the posterior as in the lateral columns. In the Monkey similar averages are 31 for the posterior and 75 for the lateral ; hence in this animal we infer that the direct fibres are at least twice as numerous in the lateral as in the posterior column.

In both animals "minimal" excitation of the anterior columns at one end of the experimental tract evokes a doubtful effect at the other end, and we infer that there are few, if any, directly continuous fibres leading in these columns between the mid-dorsal and the lumbar regions. Indeed, the cord may be divided in its anterior region* without in any way interfering with the production of electrical effects, either on the peripheral or central side of the division. Further, the application of more intense stimulation to the anterior columns although producing local movements evokes no constant electrical effects, the only results ever obtained being either with the use of considerable intensity of stimulation or with the animal but very slightly etherised. In these last cases, the magnitude of the local movements renders any strict localisation of the stimulus upon the deeply situated anterior columns impossible ; any results obtained under such circumstances we therefore rejected as absolutely untrustworthy.

It must be borne in mind that in all the preceding experiments a degree of anæsthesia was used, with which no violent movements were caused by any of the stimuli employed. How far the relations of one column to another can be detected in the unanæsthetised animal by the employment of similar methods to those now used, does not seem to us a question likely to yield fruitful results by its attempted solution. The nervous impulses generated by the direct stimulation of fibres are undoubtedly far more intense in their character than those which form the flow of the sensory and motor processes in the normal animal. This is especially true when the fibres in the posterior roots and the cord are subjected to external stimulation, possibly because some mitigating influence of the cells in the posterior root ganglion is removed. Hence, when such external stimuli are used, it is desirable that these should be of the weakest character consistent with obtaining definite results, and that the animal should be in a state of narcosis sufficiently profound not merely to cause complete insensibility to pain, but the abolition of all violent reflex movements.

The conclusions as to the conduction of nerve impulses in the cord of the Cat and Monkey, to which the study of the foregoing experimental details has brought us, are only true when these impulses are generated in the mode hitherto employed, viz., that of

* These experiments will be published in detail in a later communication in which we shall specially deal with the anterior columns.

electrical excitation of the fibres of the cord itself. We have, however, used for the sake of control, a method which did not involve such stimulation, that, namely, of injecting a dose of a 1 per cent. solution of acetate of strychnia sufficient to ensure toxic effect.

Under those circumstances, whether the upper or lower end of the experimental tract is connected with the galvanometer, marked electrical changes, evidently excitatory, are produced whenever by touching the afferent nerves of the experimental tract a strychnia convulsion is evoked. Hence the impulses thus generated in the cells of the cord pass both up and down along the nerve fibres. As to the channels in which they pass, we can only say that since a section of the whole ventral or anterior portion of each half of the cord did not sensibly diminish the amount of the electrical changes, whilst a section of the whole dorsal or posterior portion of each half of the cord did notably diminish the amount, it would seem that these channels along which the discharge of the cells passes are situated in the dorsal half of the cord, that is, in the posterior or dorsal third of the lateral columns, the posterior columns, and the posterior horns.

In another experiment of the same general kind, we divided the upper end of the cord into two halves, dorsal and ventral, as described in the method of operative procedure. (Chapter III., Section 2.) We then connected each half with the galvanometer electrodes, and observed the amount of the electrical changes in each during strychnia spasms. The changes in the dorsal half were very much more marked than those in the ventral (anterior) half, thus not only confirming our previous conclusions that the nerve channels by which the impulses were conducted were situated in the dorsal half of the cord, but also suggesting novel considerations as to the source and direction of discharges of nerve energy in the cord. (See Chapter XI.)

This experiment being rather framed to control our method than to ascertain channels of discharge, must not however be considered as conclusive.

Finally, it will be noticed that we do not attempt to differentiate between the different columns of nerve fibres which are situated in the lateral column, direct cerebellar, antero-lateral, pyramidal, &c.

We will now pass on to consider the electrical changes evoked in the cord, not by stimulation of its own fibres, but those of its nerves.

CHAPTER IX.—ON THE ELECTRICAL EFFECTS EVOKED IN THE SPINAL CORD BY EXCITATION OF THE LUMBAR NERVES.

Section 1.—Introductory.
Section 2.—Results of Preliminary Experiments.
Section 3.—Present Knowledge as to the Conduction of Afferent Impulses by the Spinal Cord.
Section 4.—Anatomy of the Lumbar Plexus in the Cat and Monkey.
Section 5.—Method involving Intervening Sections.
Section 6.—Influence of Hemisection.
Section 7.—Section of Posterior Columns.
A. Both Columns.
B. Column same side as Nerve.
C. Column opposite side to Nerve.
D. Section some time previous to observation.
Section 8.—Section of the Lateral Columns.
Section 9.—Summary of Results.

Section 1.—Introductory.

The presence of excitatory processes in the bundles of nerve fibres which compose the spinal cord is characterised, as the experiments detailed in the preceding section have shown, by very definite electromotive changes. It is thus possible to extend the field of enquiry which the estimation of the amount and character of these changes has opened up, so as to embrace not merely the relations of the fibres in one portion of the cord to those in another portion, but the relations of these to the entering and issuing nerves. The importance of obtaining some definite data with reference to these questions will be obvious when it is remembered that there is hardly any subject in which the evidence is at once so conflicting and so unsatisfactory as that of the paths by which afferent and efferent impulses travel from and to their respective nerve roots. If the present method of observing the excitatory electromotive effects is a trustworthy guide to the presence and amount of nerve impulses in the particular region connected with the galvanometer or electrometer, then there is every hope that its application in experiments, designed to show the relations now referred to, will be one from which definite results may be expected. How far this is borne out the following experimental details will indicate, but it may be at once stated that the procedure has not belied its promise, and that, by applying still more accurate and delicate methods of the same kind, there is every reason to suppose that in the future results still more definite will be obtained, and that the actual differentiation of the afferent from the efferent fibres in their course through the bulbo-spinal system will thus be arrived at. In this manner another method will be secured for research into the anatomy of the central nervous system.

We must again note that there are two considerations concerning the functional causation of any excitatory process in the cord, that of pure conduction in fibres, and

that involving the activity of the corpuscles. If, then, on exciting a mixed nerve it be found that excitatory processes are present in a distant portion of the cord under investigation, these may be due to—

(1.) The propagation of these processes from the point of stimulation along direct and continuous nerve fibres which pass into the cord and on through the investigated region ;

(2.) To the reflex discharge of interposed cells in the cord, brought about by the arrival of excitatory processes which, having travelled up the nerves from the point of stimulation, have entered upon paths ending in cells. These cells being thus awakened, themselves start nerve impulses which travel on up the cord, and, reaching the investigated area, produce the observed electrical effects ;

(3.) To the mixture of effects produced by impulses both in direct paths and the indirect ones just described.

It must, therefore, be borne in mind throughout the present research that these different causes may be operating in the production of the electrical effects observed ; hence, one of our first experimental enquiries was to endeavour as far as possible to discriminate between the effects referable to the direct fibres actually excited, and those which were related but indirectly with these fibres, being primarily associated with channels connecting the area of investigation with corpuscular mechanisms in the cord.

This we have attempted to do by employing such a low intensity of stimulation as should in any particular degree of narcosis be sufficient to evoke nerve impulses, as evidenced by electrical changes, and, at the same time, not so intense as to arouse any sign of reflex movement. The weak impulses thus generated in the excited nerve presumably pass for the most part, if not entirely, along direct nerve fibres in the cord which are not in relation with nerve cells before arriving at the region observed (mid-dorsal) ; the evidence to be detailed later strengthens this presumption.

The subject matter now dealt with really comprises the whole question of the relation of the bulbo-spinal system to the lumbar nerves. It is obvious that this relationship is one which may be discussed under three heads according to the particular part of the nerve tract under observation.

First, the characters of the nerve impulses which pass along the channels of the cord after entering it by its nerve roots ;

Second, the characters of the nerve impulses which, aroused by excitation of the channels of the cord and passing out into its nerve roots, descend along fibres of the mixed nerve ;

Third, the characters of the nerve impulses which enter and leave the cord by virtue of its so-called central structures and their various connections.

Of these three groups, the first alone will be treated of in the present chapter, the second and third being reserved for Chapters X. and XI. respectively.

Section 2.—General Plan and Results of Preliminary Experiments.

The experiments to be referred to in this chapter were made upon both Monkeys and Cats, and all involved the following operative procedure. The spinal cord of the etherised animal was exposed in the lower dorsal region; it was then divided and prepared on the peripheral side of the section for 4 centims., so that the upper end of this lower fragment of cord could be raised from its canal and attached to the cables of the non-polarisable electrodes as described in the previous sections. The galvanometer circuit was then brought by one electrode into relation with the cross section of the cord, by the other with a ring of longitudinal surface at about a centimetre distance. (See Plate 29.)

The two sciatic nerves were now exposed and divided, so that they could be raised and the central end placed, when desired, upon a pair of platinum electrodes (see p. 301 and fig. 3), precautions being observed in their preparation with respect to maintenance of circulation, drying, &c., as indicated at length in Chapter III.

If the large and persistent resting electrical difference between the cross section and surface of the cord be balanced, and the galvanometer needle thus brought into its zero position, then on exciting the central end of either sciatic nerve for 5 seconds with the interrupted induction current (Helmholtz side-wire), an electrical change occurs in the cord, the surface contact becoming galvanometrically negative to the cross section.

On the cessation of the excitation, the needle rapidly returns to its original point and, in most cases, then continues to slowly move to a position upon the opposite side of the zero, thus indicating that the excitatory negative change only lasts as long as the excitation, but is succeeded by a more lasting after-effect of opposite sign. This increase in the resting difference has been already alluded to in Chapter IV. Errors due to any electrical escape are mimimised by the nature of the excitation, and the position of the galvanometer electrodes (see Chapter III., Section 4); moreover convincing proof that the effect is truly an excitatory one is afforded by the following facts:—

(1.) A similar negative change occurs when, with the sciatic nerve uncut, the skin over the foot is pinched with ivory or touched with a hot glass rod;

(2.) A sudden change of small amount, but similar in sign, is produced when the nerve is mechanically excited by a ligature, cut, &c.;

(3.) Very pronounced effects of similar sign occur when, after injection of a few drops of a 1 per cent. solution of strychnia acetate, the nerves connected with the lower part of the cord are mechanically excited.

The electrical change in the cord is thus excitatory, and its resemblance to that in nerve warrants the presumption (see p. 277) that it is due to the passage of excitatory impulses along nerve fibres present in that portion of the cord with which the galvanometer is connected.

Etherisation.

These nerve impulses may, as before stated, have two direct sources of origin, namely, the excited mixed nerve or the grey matter in the cord, which the arrival of afferent impulses may have thrown into functional activity. They may be conducted along direct fibres from the lumbar nerves to the dorsal cord or to central mechanisms, and from these either along continuous fibres to the area observed or along short internuncial fibres to other cellular mechanisms, and so again to others and thus finally reach the area.

That the change is due to the presence in varying degrees of all these three factors is extremely probable from anatomical considerations, since GAULE* has shown that the number of fibres in the Frog's cord can be satisfied by such a triple arrangement. It is, moreover, clear, from the influence of profound etherisation upon the electrical change, that, when an adequate strength of stimulus is employed, the galvanometric effect varies in amount with the pronounced or slight character of the visible reflex effect. This has been already referred to (p. 372), but its importance in connection with the subject of this section warrants the introduction of some experimental details. We therefore give as examples the following:—In one case, on exciting the sciatic of a profoundly etherised animal (Cat) with a weak but adequate stimulus for 5 seconds, the galvanometric cord effect was 76 scale; the animal was then less etherised and the effect was 220 scale. On again deeply etherising the effect with the same excitation sank to 130; upon the ether being then more or less removed, the excitation produced an effect of 200; whilst on renewed profound etherisation this was only 80. In all these cases very feeble reflexes or none were observed in the profoundly etherised animal, but the reflexes were well marked when with less narcosis the larger electrical changes were noted.

These differences evidently point clearly to the fact that the electrical change may not only be that due to the transmitted nerve impulses up direct tracts, but also to the presence of interposed cellular mechanisms and their susceptibility of response to the arrival of afferent impulses. In Chapter III. we have discussed the value of the use of ether as a means of discriminating between the functional activity of fibres and of fibres *plus* cells, to that chapter we refer the reader, merely remarking now that we must not lose sight of the fact that etherisation, especially when very profound, may affect the nature of the excitatory processes in the nerve fibres themselves, as in the experiments made on the nerve of the Frog by BIEDERMANN with ether vapour. The differences between effects obtained with unvarying intensity of stimulus but different degrees of narcosis are practically the same as those obtained with different strengths of excitation and unvarying but not too profound anæsthesia.

* GAULE, 'Abhandl. Math.-Physik. Classe d. Kgl. Sächs. Gesellsch. d. Wiss.,' 1889 (vol. 15, No. IX.; 'Neurol. Centralblatt,' vol. 9, p. 3.

Relation of Effect to Strength of Stimulus.

To ascertain this relationship, the practice we employed was to use an initial strength of stimulus which was just sufficient to produce a cord electrical effect when applied to either nerve with the animal efficiently narcotised, then to follow with a stimulus of double that intensity, and observe the now increased value, and finally to proceed by doubling the strength of stimulus until a point was reached when the effect was only slightly altered. Such an experiment is the following one made upon the Cat. An initial excitation for 5 seconds with the secondary coil at a distance of 500 (see Chapter III. on experimental method and apparatus) gave a cord effect indicated by a galvanometric deflection of 65; similar excitation of twice the intensity, 1000, gave a cord effect of 122, and an excitation of four times the intensity, 2000, gave a cord effect of 152. In the Rhesus Monkey a similar result was observed; thus an initial excitation for 5 seconds of the sciatic nerve, with the coil at 2000, gave a cord effect of 32 (galvanometer deflection), whereas twice the intensity of stimulation, 4000, gave 60, and three times the intensity, 6000, gave 78. These selected individual examples furnish data which are strictly in accordance with the average effect as deduced from all the observed instances which occur in our experimental records. Thus if we select all the unexceptional readings of galvanometric cord effects obtained in both Cat and Monkey with the initial strength of stimulus, the average of seventeen is 56; similar readings (twelve instances) with twice this strength of stimulus give an average of 100; whilst the average of sixteen instances with four times the initial strength is 168. It is thus evident that the cord effect increases with the intensity of the stimulus at first in direct proportion to the strength, but afterwards in one less directly related with this factor. A point is ultimately reached at which no increase, but a decrease, in cord effect occurs. This, it need hardly be said, is partly dependent upon the damaging effect of the stronger exciting current upon the stimulated nerve, and partly upon the fatigue of the cord cells through the arrival in the cord of the very intense nerve impulses evoked by the strong stimulus. In these experiments, as in all others to be referred to in this section, the number and characters of the successive stimuli employed were the same in each case. (See Chapter III. Section 3.)

It is remarkable how close the amounts of the different cord readings obtained in various individuals of one species are to one another, and how often, especially in later experiments, the initial intensity of stimulus required with different nerves and different animals was the same (500 coil), thus showing the similarity of the narcosis. We may here draw attention to the minimum and maximum effect obtained in the Cat, the first with the coil at 500 and the second at 2000; the minimum being 20, the maximum 340. So far then as the relation between the size of the cord effect and the strength of the nerve stimulus is concerned, there is a strong resemblance between a nerve-to-cord excitatory electrical change and that in a nerve; the ether effect before-mentioned

indicates, however, a difference, since we have not as yet observed in the Cat or Monkey any such very marked change in the excitatory effects in purely nerve preparations as definitely dependent upon the degree of etherisation.

The absolute determination of the true character of the minimal cord effect, and the question to what extent it is to be considered as entirely due to the propagation of nerve impulses along direct and continuous paths, unmixed with impulses generated in nerve centres, might be settled by accurate experimental observations upon the time relations of the cord electrical change, particularly the time of its development relation to the seat of nerve excitation. Such an enquiry would doubtless involve the use of Bernstein's differential rheotome, since the small size of the minimal effect is a serious objection to the use of the much simpler method of recording by photography the movement of the meniscus of a capillary electrometer.

It may be mentioned incidentally at this point that the cord effect evoked by a single electrical excitation of the sciatic nerve was, however, sufficiently pronounced to cause a distinct movement in the mercury of our capillary electrometer. The movement when magnified 300 times was just visible with a weak stimulus (coil, 500), and was quite marked with a maximal stimulus (coil, 2000). It was always a single movement, but appeared to the eye rather more prolonged in character than that which was obtained in the case of the single nerve effect as displayed in the photographs of our former paper.*

It may be asked at this juncture upon what evidence we assume that the effect in the cord, following the excitation of the sciatic nerve, is due solely to the arrival therein of nerve impulses which have travelled up posterior or afferent fibres. The evidence, which is supplied in full detail (in Chapter XI.) upon the relations of the nerve fibres and the nerve cells, shows that no electrical changes appreciable by the galvanometer can be produced in the cord by even strong stimulation of the anterior or efferent roots.

It is thus clear that stimulation of the sciatic nerve generates nerve impulses which enter the cord by the posterior roots only, although, owing to our ignorance of the influence of the spinal ganglion, it cannot be assumed that the impulses are the same in character as those generated by excitation of the posterior roots themselves. We may now pass on to the consideration of the object of our experiments.

The object of the investigation will be best set forth by considering the present position of our knowledge of the relations of the spinal cord to the lumbar nerves, and particularly to the afferent fibres of those nerves. For if we are justified in assuming that the electrical effect observed in the cord is due to the passage of nerve impulses, and their arrival at the portion of the cord under observation, then, since the method of observation is one which furnishes us with quantitative data, its employment places within the experimenter's grasp a means of ascertaining to what extent these impulses can be interrupted by definite section of any one tract of cord

* 'Roy. Soc. Proc.,' *loc. cit.*

fibres, and thus of indicating which groups of fibres in the cord form the chief channels of conveyance; and the value of this method will be manifest when the character of those previously used and the conflicting nature of their results, have been placed before the reader.

Section 3.—Our Present Knowledge as to the Conduction in the Cord of Afferent Impulses.

We have already referred in Chapter II. to the investigations made by previous experimenters in order to determine the paths of conduction in the spinal cord. It will, however, be advantageous to select the most typical of these experiments and discuss their results, in order that the scope of these methods, together with those excellencies and deficiences which each possesses, may be clearly in the mind of the reader, before the uses of that which we advocate and its results are entered upon.

The various methods may be grouped as anatomical and physiological.

I. *Anatomical.*

The posterior root fibres have been traced into the spinal cord, and a considerable number* (according to Kölliker the majority) of these have been seen to divide and send branches up and down the cord. The further course of these fibres has up to the present been traced only by the method of degeneration.

(*a.*) It has been ascertained that when, in consequence of section of a lumbar posterior root, the fibres upon its central side degenerate, the degeneration is continued in certain regions of the posterior column of the same side, such degeneration up to the present only being seen in parts above the entering root. In other words, the degenerated fibres present in the posterior root are represented in the cord above the root by certain fibres in the posterior column of the same side. These fibres are believed to be the direct continuation of some of the fibres in the root; they are situated in the postero-external column at first, but gradually shift towards the middle line as they ascend, and ultimately occupy a definite portion of the postero-median column. In addition to these fibres which appear to have a continuous course up the posterior columns of the cord, there are others which show degeneration only in the immediate neighbourhood of the entry of the root; these are situated in the posterior root zone and in the marginal zone, as well as in the postero-external column. They are characterised by only occurring in that portion of the cord which lies above the root, and by being all on the same side of the cord as the lesion. Hence these fibres, whilst in direct continuity with fibres in the root, either end (Kölliker)

* Golgi: 'Anat. Anzeiger,' vol. 5, pp. 13, 14. Ramon-y-Cajal: 'Trabajos del Laboratorio Anatómico de la Faculdad de Medicina,' Barcelona, Abril, 1890. Kölliker: "Ueber den feineren Bau des Rückenmarks," 'Sitzungsberichte d. Würzburger Phys.-Med. Gesellschaft,' 8. März, 1890.

or come into relation with cells shortly after entering the cord, the degeneration in consequence ceasing. This cessation of degeneration is indicated by the numerical superiority of the degenerated fibres in the posterior roots over those in the posterior column, and above all the postero-median column. As far as it goes the evidence itself afforded by this method is fairly conclusive; whatever other channels there may be, undoubtedly the above-named do exist, and thus the posterior column of the same side offers a direct tract up which some nervous impulses undoubtedly not only can, but do, pass.

(*b.*) A similar investigation applied to the cord, since it determines all the fibres in which degeneration is seen above the level of a hemisection, carries us a step further than the above method. In this not only the fibres just indicated in the posterior column degenerate, but all the through fibres from every root below on the side of the hemisection. Further, it marks out all fibres which have their nutritive or developmental centre, not in cells in the ganglion on the root, but in cells situated in the cord below the section. Such fibres now seen as degenerated above the lesion are grouped into two parts of the lateral column, the antero-lateral, and the direct cerebellar. Except that the former is much more diffuse, the degenerated fibres being scattered about among other sound ones, there is little to distinguish the character of these two groups except their situation. They both appear to have similar terminal connections, at any rate, on the cerebral side. They are both characterised by containing fibres of very variable length, many of which appear after a shorter or longer distance to again come into relation with nerve cells, so that in these the degenerative change ceases. The characteristics of these tracts are, therefore, twofold; they appear to afford not only a direct connection between certain cells in the cord (Clarke's column, &c.) and the peduncle of the cerebellum of the same side, but also a series of internuncial connections, by means of which cells at variable distances are brought into relation with each other.

The tracts which degenerate on the peripheral side of a hemisection are foreign to the purpose of the present chapter; one, however, may be mentioned, the so-called "comma-shaped" patch in the ventral part of the postero-external column, since it is in all probability a tract of ascending fibres which are looped downwards, the degeneration corresponding with the loop.*

As far as this evidence under (*b*) goes it is not so direct as that in (*a*). It is conclusive as showing that, if there be crossing of any of these tracts from one side of the cord to the other, such crossing must occur by means of cells, since the degenerative change does not cross. It is further conclusive in showing that there are continuous nerve fibres in these two situations. It is not conclusive as regards the physiological characteristics of the fibres, since in anatomical evidence, as in circumstantial evidence, every link of the chain must be present for the evidence to be

* Possibly these fibres are the descending branches of the bifurcating posterior root fibres, *cf.* especially Kölliker.

complete. The essential link, that of connection with the posterior roots, the fibres of which convey afferent impulses, is, however, wanting. It is, notwithstanding, highly probable that these paths (direct cerebellar and antero-lateral), are to be classed as afferent from the resemblance in extension of the degeneration to that present in the fibres of the posterior columns.

There are many considerations connected with growth, development, &c., which suggest that ascending degeneration is the characteristic of afferent, and descending degeneration of efferent tracts in the spinal cord; in other words, that the centres of growth and nutrition are also the centres of functional activity, and, therefore, in consequence of an interruption, that loss of functional activity and loss of nutrition both occur in the part on the distal side of the breakdown. The fact, however, that the cells in the ganglion on the posterior root exercise this nutritive function on the nerve fibres on both sides, although explicable in consequence of developmental relations (His) must cause some hesitation as to the propriety of accepting, without reserve, the principle that the direction of the degeneration coincides with the direction of the function. What has happened in the development of the posterior root fibres may possibly have also occurred in the case of some fibres in the cord. Moreover, it is conceivable that even with this relation between nutrition and function, ascending degenerative changes might occur in fibres which ought to be classed as outgoing, since they would lie as much on the efferent side of the central nervous system as do those of the pyramidal tract. Such fibres would be long internuncial fibres, connecting the kinæsthetic system of the lower (lumbar) centres with the efferent side of a similar system of the upper (or cervical) region. It is conceivable that such long internuncial fibres exist, and, if so, then impulses which subsequently become motor are conveyed by them. These impulses, although afferent in the sense that they are actually travelling up the cord, are analogous in character with all the motor or outgoing impulses, since they occupy that relation to the centres from which they started.

Without insisting on these hypothetical fibres, we may again point out that the anatomical evidence becomes vague when some of the links in the chain are wanting, hence all conclusions founded upon it must be used with the greatest caution. The facts which it surely evidences are—

1. That there are continuous fibres in the cord.
2. That these fibres do not cross from one side of the cord to the other.
3. That a small proportion of those situated in the posterior column are in direct connection with those entering the cord by the posterior roots.

II. *Physiological.*

If we turn now to the method of physiological experiment, there is hardly any subject in the whole realm of physiology upon which such divergence of experimental

result and interpretation exists as that of the relations between the columns of the cord and the passage of afferent impulses.

The contradictory facts set forth in the various papers on this subject are sufficient to justify the belief that many of the experiments made must have involved the presence of some factor of capricious character and uncertain action, common to most of them, and that the conclusions which the various experimentalists have drawn from their results are all vitiated by its presence.

When such a fundamental matter as that of the extent to which the afferent path lies on one or the other side of the cord is answered so differently that, according to one set of investigators (Brown-Séquard, Ferrier, &c.), it is wholly crossed; according to others chiefly crossed (Woroschiloff, Miescher, &c.); equally uncrossed and crossed (van Deen, Stilling, &c.); chiefly uncrossed (von Bezold, Mott); wholly uncrossed (Chauveau); it is plain that the method adopted is at fault and is quite inefficient for the purpose of determining the extent to which particular tracts in the cord are concerned with the passage of impulses. The reason why the different results of former investigators are so conflicting may, we think, be gathered by the careful study of the experimental method in two of the most elaborate of the series of investigations just referred to, those, namely, carried out in Ludwig's Laboratory by Miescher* and Woroschiloff.†

Although the experiments are well known to physiologists, we think it necessary to allude in a little detail to their character. Both sets of experiments were carried out on Rabbits, and in both the method consisted in the production of an intervening localized destruction of a portion of the spinal cord, and in then ascertaining what changes this destruction produced in the reaction of some more central portion of the nervous system of the animal to the stimulation of the afferent nerves of the distal portion. The reaction observed was, however, different in the two cases, it being in Miescher's experiment the rise of blood pressure due to the activity of the so-called vaso-motor centre of the medulla being awakened; in Woroschiloff's, the movement of the upper limbs of the animal, due, as he believed, to the awakening of a convulsive centre in the medulla. The index used by Miescher being the amount of blood pressure, had the great advantage that it varied with the strength and duration of the afferent stimulation, and thus a quantitative comparison between the results of two series of stimuli was possible, and it is, perhaps, due to this that the facts have been held as affording data of so cogent a character. They show first that the reaction of the centre, as indicated by rise of pressure, is very largely reduced when the lateral column on the opposite side of the cord to that of the excited sciatic nerves has been divided; and second, that when a complete intervening division of the cord, with the exception of one lateral column, is made, the reaction still persists, being most marked when the distal nerve on the side of the complete section is

* 'Ber. d. Sächs. Ges. d. Wiss., Math.-Physik. Cl.,' 1870. Also 'Arbeiten a. d. Phys. Lab.,' Leipzig.

† 'Ber. d. Sächs. Ges. d. Wiss., Math.-Physik. Cl.,' vol. 26, 1874.

stimulated. From this it was concluded that the spinal path for those afferent nerve impulses which, proceeding up one sciatic nerve into the cord, subsequently reached the vaso-motor centre, was chiefly contained in the lateral column of the side of the cord opposite the nerve. The experiments of WOROSCHILOFF extended these, and showed that movements of the upper limbs could be only aroused in response to stimulation of the skin of the lower limbs, provided that the lateral columns were intact; that destruction of the continuity of other portions of the cord did not notably influence the reaction; that when one lateral column was divided, the skin stimulation on the side of the lesion produced a greater reaction than that on the side opposite the lesion; and that when the whole cord, with the exception of one lateral column, was divided, the stimulation of the skin on the side of the intact column, produced a much less reaction than did that of the skin on the opposite side. From this last experiment, WOROSCHILOFF assumed that, since the impulses were transmitted from the lower to the upper portion of the cord by the bridge of fibres in the intact lateral column, they travelled throughout along such fibres in one continuous path, keeping entirely to the lateral column. The difficulties involved in this assumption, and the unsatisfactory character of the experiments, are ably set forth in a recent edition of FOSTER'S physiology, to which the reader is referred.* The conclusions, therefore, to which WOROSCHILOFF arrived were that afferent impulses were transmitted entirely by fibres contained in the lateral columns; and that by far the chief part were transmitted by the fibres in the lateral column on the opposite side to the entering nerve. By his first conclusion, he therefore placed both the posterior columns and grey matter out of court, although the former must convey at any rate some impulses since they contain a considerable number of the posterior root fibres, whilst there being no means for the impulses to cross over from the entering roots to the lateral columns of the opposite side, except through the grey matter, this latter is assumed to be in operation by the second conclusion.

Apart from the contradictions involved in this interpretation of these two sets of experiments, the results remain as definite phenomena. In seeking to ascertain their true meaning, it is essential to realize all the conditions of the experimental procedure. Now, of all these conditions, the one which is the most important is that connected with the experimental necessity of evoking definite reactions.

These reactions, whether of vaso-motor, convulsive, or other centres, are profoundly influenced by anæsthesia. It is certain that in the unanæsthetised animal the centres are largely affected by the functional discharge of other centres, and that this influence, although by no means abolished, is diminished by narcosis. In all the experiments of MIESCHER and WOROSCHILOFF no complete anæsthetic was employed, the animals being in MIESCHER'S investigations simply curarised, and in WOROSCHILOFF'S fixed in a suitable holder.

* M. FOSTER, 'Text-book of Physiology,' vol. 3, p. 189. Also 'Arbeiten a. d. Physiol. Inst.,' Leipzig, 1874.

This being the case, the whole series of experiments are in reality a demonstration of the extent to which one complicated reflex act is influenced by the awakening in the entire nervous system of a whole series of reflex discharges. The uncertainty which must attend such a method may be illustrated by the following experience of ourselves. It often happened in the experiments described in this paper (all of which were performed under an anæsthetic), that after not merely complete section, but absolute removal of a piece of cord 1 centim. long in the mid-dorsal region of the Cat or Monkey, mechanical irritation of the sciatic nerve, and especially of the posterior roots, caused not merely movement in the upper limbs, but of the head, &c., also. This effect was an indication that the anæsthesia had become too slight, and it was immediately abolished on making the latter rather more profound. We convinced ourselves that the mechanism of its causation consisted in first a reflex of the lower limbs, and that this movement dragging on the trunk aroused a reflex in the upper limbs by pulling on the nerves of the upper fragment of cord, which in the neighbourhood of the section was in a hyperexcitable state. The afferent impulses thus started now evoked general movements by discharging the higher centres. The movements of the lower and upper limbs often followed one another so rapidly that the eye was unable to distinguish between their time of commencement; in some cases, however, particularly when the narcosis was increased, the delay between the two was quite plain, and every stage might be observed. Of what value, therefore, as regards the question of conduction in the continuous tracts of fibres in the spinal cord are the results of experiments in which the animal is under no anæsthetic at all, for the employment of curare by Miescher did not provide for the adequate exclusion of reflex centres such as can be obtained by the use of ether. Indeed, Miescher's method depended upon the maintenance of the functional activity of the reflexes. It seems to us, therefore, that this is the crucial point of the whole position, and accounts for the capricious character of the results of different observers as dependent upon different methods of investigation. The index for the arrival of nerve impulses from one side of a block in the cord to the other has always been a reflex one, and it is essential for its proper working that the reflex centres should be in an excitable condition. Since the experiments involve operating on the cord and the examination of the animal in the unanæsthetised state, within a short time of the operation there is every opportunity for abnormal conditions of the other centres (in consequence of the procedure), to influence the result; such influence is so certain from the state of the animal that the results really determine, not the localisation of afferent fibres in the cord, but the extent to which the operation has augmented or depressed the excitability of the successive central mechanisms, and the bridge by means of which the lower and upper parts of the cord communicate thus becomes chiefly a column of internuncial fibres. Moreover, almost all experiments done within a few hours of the time of operation lay themselves open to our further criticism, that it is possible for the reflex movement of the hind limbs and trunk to arouse by mechanical pull of the parts

around the seat of lesion, similar movements of the upper limbs. That such reflex movements were present in the case of Woroschiloff's own experiments, is evident from the study of the account of those evoked in the animal after the operation had been made upon the cord. Thus, in one of his experiments (VI.), the animal (Rabbit), was subjected to an operation involving the division of the spinal cord in the dorsal region, the whole cord being cut through with the exception of the lateral tract of the left side. On examining the animal an hour or two afterwards, the right hind limb was found to be paralyzed, due to section of its efferent spinal tract, this efferent paralysis being confirmed subsequently by dividing the cord below the medulla and stimulating its distal cut section when only the left hind limb responded; notwithstanding this, pressure on either foot caused movements in both hind legs. Now in this case the movement of the right leg must obviously be a reflex effect, having its central physiological seat in the lower fragment of the cord, and any arguments based upon the amount of movement of the respective limbs, must deal with the question as to the extent to which the section has heightened or depressed the normal excitability of the reflex centres in this lower fragment. But it is precisely this question which it seems to us has not been sufficiently dealt with in the text, there being a tendency to treat the cord in an unanæsthetised animal as if one of its main physiological characteristics, reflex excitability, were in abeyance in the distal, though not in the proximal and central portions. The evidence cannot, therefore, be considered as adequate to warrant his statement: "Meine bis dahin vorgelegten Beobachtungen bestätigen und erweitern die Angaben von Miescher, Nawrocki und Dittmar, denn von nun an sind wir darauf hingewiesen, die Bahn, welche das Gehirn mit allen Nervenwurzeln verbindet, in dem Seitenstrange zu suchen."

The criticism just advanced is not a new one since it forms the basis of the objections of Chauveau, Schiff, and others. Its cogency is increased by the discovery made by Fodera of hyperæsthesia after section. The most important points in connection with this for our present purpose are those brought out by experiments made by Schiff* before the observations just referred to. These were, that in many cases of hemisection of the cord there is not merely hyperæsthesia below the lesion on the side of the section, but heightened reflex excitability of the cord in the neighbourhood of the lesion both above and below. This hyperexcitability is less marked when the whole cord is divided, than when a bridge joins the parts above and below the lesion. It has been found by Martinotti† that the hyperæsthesia is particularly bound up with injury of a particular region in the lateral column, and it is attributed by him not to a direct increase in excitability, but to the removal of inhibitory, *i.e.*, depressant, influences by the section. It may be pointed out that, as regards the nerve trunk, the experiments of Hering show conclusively that the increase of

* Schiff, 'Lehrbuch d. Physiol.,' 1859.

† Martinotti, "Hyperæsthesie nach Verletzung des Halsmarkes," 'Archiv f. Anat. und Physiol.' (*Physiol. Abth.*), 1890.

excitability therein caused is in direct causal relation with the electrotonic effects of the resting or persistent nerve currents produced between the cross section and the surface of the nerve trunk. Since similar electrotonic alterations in excitability have been shown to exist in the case of the spinal cord, it is most probable that a direct increase would be produced by the very large resting currents which (see Chapter IV.) have been found by us to be produced by cross sections of the cord. In this connection we may draw attention to the following striking phenomenon described by SCHIFF,* and which in the progress of the present research we have had the opportunity of seeing ourselves. We often saw that after complete section of the cord and the removal of a piece 1 centim. in length in the region of the 8th dorsal vertebra, when the animal was asphyxiated on the completion of the investigation, a sudden prolonged discharge of the nerve centres in the lower portion of the cord occurred. This revealed itself by the rising up of the tail of the animal, and its maintenance in an erect position for one or two minutes. The discharge and its effect then subside to be followed in two or three minutes by a second feebler one, and this by a third still more feeble. In addition to this it often happened that during an experiment on such a preparation, rhythmical discharges of the centres in the lower portion of the cord occurred after the section, evidenced by rhythmical contractions of the anal muscles. This has also been noticed by several investigators.

Further, in one animal (Cat 325) in which the cord was divided at the 13th dorsal vertebra, although the tail phenomenon did not spontaneously appear, when the animal was asphyxiated, it was readily evoked in full strength by slight stimulation of the skin of the tail.

These phenomena afford a striking instance both of the hyperexcitable state of the centres in the lower portion of the cord and of the capacity of these centres to discharge such a series of nerve-impulses as will produce sustained co-ordinated movements.

The difficulties thus involved in the experimental methods of MIESCHER and WOROSCHILOFF are to a great extent obviated by experiments in which, a given lesion of the cord having been made with all due antiseptic precautions, the wound has been allowed to heal, and the animal examined carefully at varying intervals, from a few days to weeks and months, after the operation. Such an experiment is that made by FERRIER† on the Monkey, in which a hemisection at the level of the 8th dorsal was followed by complete insensibility below, on the side opposite the lesion, to every form of sensory stimulus, whilst the sensibility on the same side remained unimpaired. This experiment is similar to the paralysis on the same side, and anæsthesia on the opposite side, observed in some cases of injury or disease localised in one half of the spinal cord. Other observers, notably MOTT,‡ have, however, obtained results which

* SCHIFF, PFLÜGER'S 'Archiv,' vol. 30, 1883, p. 202.

† FERRIER, 'Brain,' 1884.

‡ 'Proceedings of the Physiological Society.' 'Proceedings of the Royal Society.'

vary between partial accordance and complete opposition to the above. It is not our object to endeavour to reconcile this apparently conflicting evidence, but we may point out that great difficulties are involved in the application of the tests necessary to determine the sensibility of animals. In our own experiments, which have been made upon Cats, and which involved hemisection of the cord, the application of the water and other tests to the skin indicated that the afferent stimulus was conveyed from both hind legs up the cord, but with much greater certainty, and, judging by the quickness in the evoked movement, with much greater intensity, on the uninjured side than on that corresponding with the lesion.

It is evident that the flaw in all these methods is the fact that, owing to the index of the arrival of impulses above the lesion being some movement, the central structures of the nervous system must be sufficiently excitable to be capable of responding, and the stimulus used must be intense enough to arouse discharges of sufficient magnitude to evoke definite muscular movements.

Whilst the same flaw in the classical experiment is also present in the case of efferent tracts, its presence here does not produce such a blurring of the result, since the method can always be checked by a concluding experiment involving division of the cord below the medulla, and excitation of its distal portion, with observation of the amount and character of the movements of the lower limbs. Although acknowledging to the utmost the value and precision of the experiments carried out in LUDWIG'S laboratory, we must express our conviction that, as regards the conduction of afferent impulses, they do not warrant the inference either that the lateral columns contain the fibres of the afferent tract to the exclusion of the grey matter and the other columns, or that the fibres which they do contain form a continuous afferent path, it being quite possible that those fibres which undoubtedly conducted at the point of section were merely acting as internuncial links between distal and proximal portions of the grey matter. This latter was, by the exigencies of the method of observation, often, if not always, thrown into a state of abnormal excitability; and in the neighbourhood of the section this state was that of hyperexcitability.

It will be gathered from what has been said that the question of the relations of the fibres in the cord to the posterior roots can, in our opinion, only be arrived at by the use of a method which allows of discrimination between events taking place in the cord itself when, by means of complete anæsthesia, the activity of the reflex mechanisms is subdued. Such a method is that of ascertaining the electromotive changes in a portion of cord following stimulation of the afferent nerves, since the animal may be so profoundly anæsthetised as to give little or no reflex muscular contraction, and yet distinct effects can be detected in the cord. It is because the conclusions to be drawn from our results clash so markedly with those of MIESCHER, WOROSCHILOFF, &c, that we have thought it necessary to preface their introduction into this section by this detailed criticism. This divergence in the conclusions and the importance of the effective application of a method which besides the above advan-

tages has the greater one of furnishing us with the results of cord changes expressed quantitatively, and, therefore, capable of strict comparison with one another, have combined to cause us to devote a very large proportion of our experimental investigations to the subject of the present and the succeeding chapters. The subject matter of the present chapter becomes, therefore, an answer to the question, to what extent are the electrical changes in the cord, and hence the nerve impulses, of which these are the index, interrupted when between the stimulated nerve and the observed region of the cord different intervening localised sections are made. The principle is, therefore, that of the experiments carried out in LUDWIG'S laboratory, it is the index alone which is novel.

SECTION 4.—ANATOMICAL RELATIONS OF THE LUMBAR NERVE.

Since in all the experiments which bear upon the relations of the spinal cord to its nerves the sciatic was chosen, it is desirable at this stage to refer to the anatomical relations which exist between this and the roots of the lumbar and sacral nerves.

These differ in the two sets of animals used, Cat and Rhesus Monkey, and as we are unable to find that the comparison of their anatomical and physiological relations has been anywhere* set forth, we must proceed to examine the case of each species of animal in a little detail.

In the Cat the photograph of the plexus (Plate 35) shows that of the two branches of the sciatic nerve (*I.P.* and *E.P.*), internal and external popliteal, the former derives most of its fibres from the 6th, the latter from the 7th lumbar roots. Since the portion of sciatic nerve which we used was that in the thigh, the fibres involved were almost entirely those derived from the 6th and 7th lumbar roots, a few fibres coming from the 1st sacral, and still fewer from the 5th lumbar. The obturator nerve derives its fibres from branches of the 5th and 6th lumbar nerves, the anterior crural mainly from the 5th, but to some slight extent from the 4th.

In the Monkey the relations are somewhat different, as will be seen by referring to the photograph of the lumbar plexus of the *Macacus rhesus* (Plate 34). It will be then found that the two branches of the sciatic nerve (*I.P.* and *E.P.*) derive their fibres from a more widespread origin. The majority of fibres come from the 5th, 6th, and 7th lumbar; a few fibres from the 1st sacral join to form the trunk of the nerve, but these appear to pass entirely into that branch which leaves the trunk high up and supplies the hamstring muscles (*Hs.*). The obturator nerve derives the majority of its fibres from the 4th lumbar, receiving a few fibres also from the 5th, whilst the anterior crural derives its fibres from the 4th, 3rd, and (?) 2nd in decreasing amount.

Roughly speaking, therefore, the relations of the lumbar plexus in the two species of animals differ in this respect, that with the same number of lumbar nerves (7) the

* While this is passing through the press a very valuable paper, giving the anatomy of the plexus in the Cat, has appeared, viz., LANGLEY, 'Journal of Physiology,' vol. 12, No. 4, 1891.

main supply of each nerve is, in the case of the Cat, one root lower than in that of the Monkey.

The physiological connections of the roots were of importance to us only as far as the fibres in the sciatic nerve were concerned. In attempting to ascertain these connections it occurred to us that the electrical method would furnish a valuable means of ascertaining to what extent the fibres in any nerve trunk are derived from particular roots, whether anterior or posterior. All that is necessary for the carrying out of such investigation upon the sciatic nerve is to expose the cauda equina of an anæsthetised animal, then to prepare the nerve, divide it, and connect its isolated central end with the galvanometer. The various roots of the lower lumbar nerves are now divided at their termination in the spinal cord, and their peripheral ends excited with the interrupted induction current for a given time (5 seconds). If electrical effects are evoked in the central end of the divided sciatic, then, obviously, the root excited contains nerve fibres which pass down the nerve as far as the region observed. With the animal in a state of uniform narcosis, the comparative amounts of the deflection produced by applying to the different roots a stimulus of unvarying intensity and duration indicate the relative amount of fibres, provided that the excitability of the various roots is approximately the same. In this way we ascertained that the effect evoked in the popliteal region by exciting the peripheral ends of the cut anterior or posterior roots of the 1st sacral nerve was, in the Cat, comparatively small, being only one-sixth of that evoked by exciting those of the 7th or 6th lumbar, whilst excitation of the 5th and 4th lumbar was followed in the Cat by very little effect at all in the nerve. Physiological experiment thus bears out the anatomical details displayed by dissection. One obvious use of the method which the few experiments which we have carried out on this line suggests is, that it not only secures an analysis of the different fibres which pass from a complicated plexus into a nerve, but places within the experimenter's grasp a method of determining to what extent the relations of the afferent fibres of a nerve with the nerve roots are similar to those of the efferent fibres.

We will now turn to our experimental results made upon the cord itself.

Section 5.—The Operative Procedure involved in the Method of Sections intervening between the Observed Cord and the Excited Nerves.

The experiments were made upon twenty-two Cats and three Monkeys, and were all conducted in the following way. The cord of the anæsthetised animal was exposed and divided in the lower dorsal region, the particular locality varying from the levels of the 8th to that of the 11th dorsal vertebræ. It was then prepared for 4 centims. on the distal side of the section and connected at its cut and longitudinal surface with the non-polarisable electrodes by cables, in the same manner as that already described. (See Chapter III., Section 3.) The sciatic nerve was then exposed, freed for some distance, ligatured, and divided. It was left in the muscles

in order to avoid cooling, &c., and only taken out of its muscular bed for purposes of excitation. The large resting electromotive difference between the surface and cross section of the cord having been balanced, an excitatory electrical effect in the opposite direction to the difference was observed to accompany the stimulation of the nerve. The amount of this effect, as indicated by the amount of the galvanometric excursion, varied, as previously stated, not merely with the intensity and the duration of the stimulus, but with the condition of anæsthesia, &c., of the animal. If care be taken to keep these factors as far as possible unchanged, the excitatory electrical effect thus produced at each repetition of the experiment keeps very fairly uniform, as much so in point of fact as in similar experiments upon Mammalian nerve trunks. When we had thus obtained a constant effect in the cord, an intervening section was made in the lower dorsal or upper lumbar region by the method described in Chapter III., Section 2. Its position coincided, in some cases, with the lowest portion of the part of the dorsal cord exposed for connection with the galvanometric electrodes, in the majority of cases with a still lower level obtained by a fresh exposure of a small portion of cord. It was found that it was not desirable to make this second exposure when the cord was first prepared, since during the time lost in the preliminary experiment, &c., the intervening cord at this point is apt to suffer.

The intervening section having been thus made, the nerve was excited under precisely the same conditions as before, and the alteration, if any, in the amount of the cord effect noted. In all such experiments the extent of the section of the cord, and thus the part involved in the interruption, is capable of great variation, and the results may with advantage be grouped in relation to the particular regions which have been involved in it, thus following the exact and strictly logical method which, under LUDWIG'S guidance, was such a characteristic feature in WOROSCHILOFF'S treatise.

SECTION 6.—THE INFLUENCE OF HEMISECTION.

The results of a hemisection made between the portion investigated and the entry of the stimulated nerve as regards its influence upon the electrical changes in the cord, which are evoked by the nerve stimulation, will be best seen by a glance at the subjoined table, which gives the result of the comparative observations made in the manner previously indicated in two animals before and after the section. The animal was in all cases carefully anæsthetised and kept well under the influence of the anæsthetic; the stimulus was always in any two comparative results adjusted to the same degree of intensity, and was of the same duration, whilst, as far as possible, errors due to variations incidental to the application of the stimulus, the condition of the animal, and the galvanometric condition of the observed region of the cord, were excluded, and observations in which contemporaneous changes in either of these three conditions could be detected were rejected.

Result of Hemisection.

Excitation on same side as Section.

	Deflection.	
	Before.	After.
Cat (*a*) (349)	185	29
Cat (*b*) (327)	105	45
	132	24
Total . . .	422	98
Ratio	100 to 23	

Excitation on opposite side to Section

	Deflection.	
	Before.	After.
Cat (*a*) (349)	182	165
Cat (*b*) (327)	82	90
	142	91
Total	406	346
Ratio	100 to 85	

In Cat (*a*) the cord was divided and prepared at the lower border of the 9th dorsal vertebra, and the section made at the 13th dorsal. In Cat (*b*) the cord was divided and prepared at the 9th dorsal. Both sciatic nerves were prepared, and first one and then the other excited in the manner previously described. The stimulus was in the above cases that of the Helmholtz side-wire, 100 stimuli per second, continued for 5 seconds with an intensity just sufficient to evoke slight reflex effects in the lower part of the cord, *i.e.*, the secondary coil was placed at 500 or 1000. The ratio of the sum of the two different columns indicates that an intervening hemisection, when on the same side as the excited nerve, will diminish the cord effect 77 per cent., and that when it is on the opposite side it also diminishes the effect, but to a very much less extent, namely, only 15 per cent.

As far then as the nerve-to-cord effect is concerned, its production is very largely dependent upon the unbroken integrity of the fibres and grey matter along that side of the spinal cord with which the stimulated nerve is connected.

It is thus clear that in the etherised animal the excitatory electrical change is conducted along the structures on the same side of the cord as the excited nerve, and if the effect is a true indication of the passage of nerve impulses along nerve fibres in that portion of the cord connected with the galvanometer, then these nerve impulses themselves must be for the most part confined to that side of the cord which they enter. Further, if we assume that the readings furnish us with data for a quantitative comparison of the amounts of the variously awakened physiological activities on the two sides of the cord, and thus of the number or intensity of the afferent nerve impulses, then this preliminary set of observations would seem to indicate that from four to five times as great a volume of excitatory change flows up the cord on the side of entry of the nerves as on the other.

This result is fully in accordance with the anatomical evidence previously referred to, and with the results of spread obtained in the cord by excitation of its own columns detailed in Chapter VIII. It is in absolute opposition with the before mentioned results of MIESCHER and WOROSCHILOFF.

The indications of these experiments are confirmed by a large amount of collateral evidence dependent upon the influence of section of the various columns. This will be seen as we detail in succession the results of our different lesions.

Previous Hemisection.

In order to ascertain whether this loss on the side of the lesion was independent of all functional changes due to the shock of the operation, &c., the hemisection was made, in two instances, a considerable time (thirty days and more) before the experimental investigation.

On the first animal, Cat (283), the hemisection had been made four months previously at the level of the 12th dorsal vertebra on the left side. Before commencing the experiment the animal was carefully examined both in its normal condition and under an anæsthetic. The left hind limb was dragged in walking, and showed marked loss of muscular power. On allowing the feet to touch cold water movements were started, the right hind leg being smartly drawn up, the left only after a considerable delay. This and other tests applied to each foot indicated no impairment of sensibility on the right side (that opposite to the lesion), but considerable impairment of both tactile sensation and movements on the left, the same side. On placing the animal under an anæsthetic the left knee jerk was seen to be much exaggerated, and it was possible to start clonic spasms in this limb.

For the actual experiment the cord was divided at the level of the 7th dorsal vertebra and the upper end of the lower fragment prepared for connection with the galvanometric electrodes. The electrical effect produced by exciting each of the two prepared sciatic nerves was now observed, the stimulus used being of minimal and maximal intensity respectively and consisting of the usual series of induction currents, 100 per second for 5 seconds.

SECONDARY Coil 500 (minimal).

	Excitation of right nerve. Side opposite lesion.	Exeitation of left nerve. Side of lesion.
Cord effect	90 90 95	20 28 45
	Average 92	Average 31

The electrical change is thus three times as large when evoked by stimulation of the nerve on the side opposite to the lesion, that is, the right side, as on the side (left) of the division. Hence, the major part of the change must be cut off on the left side by the lesion,* that is to say, the nerve impulses, of which the change is an index, are unable to ascend the cord on the left side to the observed region in the neighbourhood of the 7th dorsal, owing to the hemisection at the 13th dorsal interrupting their path. If we suppose that the actual effect observed by stimulating the left nerve is due to impulses which normally cross the cord, whilst that observed by stimulating the right is due to impulses which do not cross, then the interruption has cut down the effect which the normal excitation of the left sciatic nerve would produce from $92 + 31 = 123$ to 31, *i.e.*, 75 per cent.

When the stimulus was four times the intensity of the above, that is, sufficient to evoke strong reflex contractions, a similar disproportion was found to exist although it was not so marked.

This is shown by the following table:—

SECONDARY Coil 2000.

Excitation of right nerve.	Excitation of the left nerve.
340 215 220	170 160 135
Average 258	Average 155

* In this animal microscopical examination of the cord showed that the lesion involved all the left lateral and posterior columns, the whole grey matter, and, except its median edge, the anterior column. Of ascending degeneration there was beautifully marked destruction of the left postero-median column, as also of the direct cerebellar and antero-lateral tracts, and a few degenerated fibres in the right postero-median column. Of descending degeneration there was, immediately below the lesion, degeneration in the left lateral pyramidal tract and also in left the anterior column.

The effect even with this strong stimulus is nearly twice as large when evoked by the nerve opposite to the side of the lesion. Since, however, a considerable effect is evoked by stimulation of the nerve on the same side, the use of the stronger stimulus has either produced more impulses strong enough to cross the cord, or it has caused a more complete discharge of the central mechanisms in the grey matter.

The other animal, Cat (259), had a section made upon it at the 10th dorsal vertebra thirty days before the observations were to be made. The section involved the left lateral and the majority of the left posterior column. The subsequent examination of the cord showed that the section involved on the left side the lateral column, the ventral portion of the anterior column of the grey matter, and the dorsal half of the posterior column ; on the right side the posterior median column. The ascending degenerative changes were at the 5th dorsal traceable on the left side to a marked degree in the direct cerebellar and antero-lateral tracts, and in the posterior root zone and posterior median columns. A much less extensive degeneration was found to have occurred in the posterior median column of the right side.

The animal, when examined before the experimental observations, showed spastic paralysis of the left hind limb, and marked diminution in the tactile sensibility of both hind limb and trunk on the left side. The knee jerks were equally present on the two sides. The experimental investigation, as far as it relates to the present question, involved the section of the cord at the 4th dorsal (this was accompanied by prolonged tetanus of lower limb muscles and those of the tail), the preparation of the upper end of the lower fragment and the excitation of the two sciatic nerves. The excitation of the right nerve evoked effects of 43 and 56, the left of 15 and 22. The sum of these readings is 99 for the right, and 37 for the left side. If, as in the previous experiment, we suppose that the total sum of the two effects roughly represents the full responsive change of either nerve excitation, then the effect on the side of the chief lesion (hemisection) is reduced from that in the ratio of 136 to 37, *i.e.*, 100 to 27, that is, it has been reduced 73 per cent. through the hemisection.

The result of these experiments is to show that the excitatory changes in the cord, evoked by stimulation of the sciatic, are largely limited to the same half of the cord as the excited nerve, the amount of limitation being such that three times the effect, and presumably three times the number of nerve impulses, proceed up the cord on the side of entry than that which is evoked by impulses either crossing in the cord, or freshly generated by cells in response to the arrival of impulses in the grey matter on the opposite side.

Our method, however, enables us to determine not merely that the excitatory effects in the cord are to a great extent limited to the side of the entering nerves, but also that the effects are mainly dependent upon the unbroken integrity of particular columns of fibres on this side. To observations on this point we now pass.

Section 7.—The Influence of Section of both Posterior Columns.

A. *Section of both Posterior Columns.*

The anatomical evidence clearly shows that there is an unbroken path between some of the entering afferent fibres and the fibres in the posterior column, and that these subsequently pass more or less completely into the posterior median column from the posterior root zone. It was therefore essential to ascertain to what extent the cord effect was dependent upon the presence of these fibres. This we have endeavoured to do by first ascertaining to what extent the effect is due to the unbroken integrity of both posterior columns. A remarkable incident in the course of our experiments led us early to suspect that by far the greatest part of the effect, whether crossed or direct, is conducted along these tracts. In the course of the operation for one experiment, whilst opening up the neural canal, the point of the bone forceps slipped, and so slightly bruised the posterior columns that the injury could not be detected at the time. The preparation was proceeded with, and the cord divided at the 8th dorsal. The upper end of the lower fragment was then connected in the usual manner with the galvanometric electrodes, and the sciatic nerves exposed for excitation. Only extremely small cord effects were, however, evoked by the excitation. We then discovered the bruise and determined to make a fresh section below the injury, exposing for this purpose more cord; on connecting this fresh portion with the galvanometric electrodes and exciting the nerve, an effect of 175 scale was obtained.

We now made a direct experiment along the lines thus indicated.

The cord was exposed in a Cat, and divided at the 10th dorsal vertebra, prepared for 4 centims. and connected with the electrodes by its surface and cross section. Excitation of the left sciatic nerve, with the secondary coil at 2000 (1 Daniell in primary) for 5 seconds (500 stimuli), produced cord effects indicated by a deflection of 75 scale. The posterior columns were then divided at the level of the upper border of the 12th dorsal vertebra, and a similar excitation was accompanied by a deflection of only 12 scale. As a control, the cord was now completely divided at this latter level, and the part distant from the new section was connected with the galvanometer, when a similar excitation produced a deflection in one case of 64, in another of 75 scale, thus indicating that the great diminution of the effect was due to the local operative interference with the posterior columns, and not to any general alteration in the condition of the whole cord.

A similar result was obtained in another animal (Cat), in which the cord was prepared and connected with the galvanometer at the level of the 10th dorsal vertebra, and the cauda equina having been exposed, the central end of a cut posterior root was excited, instead of the sciatic nerve. In this case the cord effect,

which was accompanied by reflex movements, was 210 with the columns intact, and after their division at the level of the 12th dorsal vertebra, sank to 36.

In the Monkey this marked diminution was also found. Thus in a *Rhesus* the cord was divided at the lower border of the 6th dorsal vertebra, and prepared as before. Excitation of the right sciatic nerve evoked a cord effect of 82; excitation of the left sciatic an effect of 60; after division of both posterior columns at the level of the lower border of the 11th dorsal vertebra, excitation of the right sciatic produced an effect of only 18, and that of the left sciatic an effect so small as to be indicated by a mere trace, viz., 2.

It need scarcely be pointed out that the presence or absence of concomitant reflex movements as an index of the awakened corpuscular activity of the cord is a most important factor to be borne in mind, but the diminution occurs even when a more pronounced stimulus of greater duration is used, as is shown by the following experiment on a *Rhesus* Monkey. The cord was divided at the 8th dorsal vertebra, and prepared for galvanometric observation. The right sciatic was excited and evoked a reflex movement and large effects, indicated in repeated observations by deflections of 210, 300, and 308. The left sciatic gave effects of 230, 250. After section of both posterior columns, the effect sank to 55 and 58 following excitation of the right nerve, and to 90 and 60 following excitation of the left nerve.

If now we sum up the various readings (15) obtained in two Cats and two Monkeys, we find, as expressed in the following table, that the intervening section reduces the massed results in the ratio of 100 to 22, that is, both the posterior columns are directly concerned with the production of 78 per cent. of the total effect, and the transmission of the same percentage of impulses.

TABLE of Readings. Section of Posterior Columns.

	Cord investigated at	Deflection before section.	Deflection after section.
Cat . . .	10th dorsal vertebra	75	12
„ . . .	„ „	64	12
„ . . .	10th to 11th dorsal	210	39
Monkey .	7th dorsal (average of six readings) .	96	18
„ .	8th dorsal	210	55
„ .	„	300	58
„ .	„	308	57
„ .	„	230	90
„ .	„	250	60
		1743	389
	Ratio 100 to 22.		

This relationship is confirmed by a control experiment of the reverse kind in which a

section of the part of the cord ventral to the posterior columns was made. The cord was prepared in a Cat by division at the 8th dorsal vertebra; the upper end of the lower fragment connected with the galvanometer, and the left sciatic stimulated with three different strengths of stimulus, and the effect noted in each case. An intervening section was then made at the 10th dorsal, so as to divide the whole region of the cord lying ventrally to the posterior commissure and the commissure itself, the result being that the minimal effect remained unaltered, whereas the other effects were diminished in the ratio of 100 to 76, as indicated in the subjoined table.

Strength of stimulus.	Effect before section.		Effect after section.	
500	35		35	
1000	70	100	56	121
2000	95		65	

Ratio 100 to 76.

This experiment, whilst it establishes the importance of the posterior columns by furnishing the control experiment of leaving these tracts and excluding the others, is at the same time a remarkable instance of the quantitative precision of the method, since in independent experiments lesions effected quite differently show in the one case that the posterior columns are concerned with 75 per cent., in the other with 76 per cent. of the effect. As the experimental details accumulate, this steady quantitative relation will be found to vary wonderfully little, considering the nature of the structure investigated and the difficulties connected with the method.

The experiment just alluded to also indicates a very important fact which will be referred to in detail in the concluding section of this work, namely, that when the stimulus is minimal the nerve impulses are almost entirely confined to the direct path; in other words, this path is that of least resistance. It is necessary for the stimulus to be of a certain intensity before nerve impulses can be started of sufficient volume to break through corpuscular structures and so enter on indirect paths. This is indicated by the fact that no change in the deflection could be observed in the case of the weak initial stimulus to follow the section of the grey matter; presumably, therefore, the cord effect was due, in this case, to afferent impulses passing up the direct path.

A further extension of the experiment just described may be now referred to, namely, the influence of dividing in addition one posterior column. After the section of the anterior or ventral portion of the cord the left posterior column was divided at the 10th dorsal vertebra; on now stimulating the left sciatic nerve an effect of 8 only was obtained, this observation being repeated several times. The importance of the posterior column on the side of the nerve is thus forcibly brought into view.

B. *Section of the Posterior Column of the same side as the Nerve Excited.*

The marked diminution in the effect obtained by hemisection on the same side as the nerve in the one case, and by section of both posterior columns in the other would seem to imply that the posterior column on the same side, which is common to both these lesions, is the fundamental structure concerned. We shall see that there is every reason to suppose that it is concerned with 60 per cent. of the total effect, that is, with that proportion of the number of nerve impulses, the remainder being pretty equally divided between the lateral column of the same side and the posterior of the opposite side. It will be seen that the direct evidence of the result of section of one posterior column is somewhat complicated by changes in excitability which appear to affect the remaining columns.

The results were observed in two Monkeys and five Cats, as shown in the following Tables :—

Section of Posterior Column on Same Side as Nerve.

	Cord observed at	Before section. Deflection.	Section at	After section. Deflection.
Monkey (*Macacus rhesus*)	5th dorsal vertebra	130 214 304	10th dorsal vertebra	38 66 100
Monkey (*Macacus rhesus*)	A dorsal vertebra (the 8th probably)	32 60 78	11th dorsal vertebra	12 21 14
		814		252

Ratio of 100 to 31

In these Monkeys section of the posterior column on the same side reduced the cord effect by 69 per cent., a very notable amount. Such a large reduction was not often obtained in the Cat: and occasionally in this animal comparatively insignificant reductions were seen. In such instances, however, the nerve stimulation was observed to evoke violent reflex movements, and, as will be seen in considering the result of section of the opposite posterior column, the opposite uninjured side of the cord became evidently hyperexcitable.

Section of posterior column on same side as nerve at 11th to 12th dorsal vertebra.

Cord observed at 8th dorsal.	Deflection before section.	Deflection after section.
I. Cat	90	35
II. Cat	100	38
	75	34
III. Cat	76	45
	83	24
IV. Cat	210	115
V. Cat	185	96
	185	121
	1004	508
Ratio of 100 to 50.		

The above experiments made upon five Cats give results, which, as is seen, differ considerably in several instances, the deflection before section being in some cases four times as great as that after section; in others not twice as large. The latter is, however, the case when owing to some circumstance the stimulus evoked very large effects (see Cats IV. and V.) including strong reflex movements. If, however, we mass together all the results obtained in the two sets of animals, the average reduction of effects due to section of one posterior column would amount to about 60 per cent. of the total effect obtained in the normal condition. Hence it would seem that one posterior column is the main channel by which the entering nervous impulses proceed from the lumbar to the dorsal cord.

The difficulties involved in this series of experiments will be still more evident when we turn to the influence of the section of only the opposite posterior column upon the cord effect.

C. *Section of the Posterior Column of the Opposite Side to the Nerve Excited.*

In these experiments we are for the first time confronted with the remarkable fact that in consequence of an intervening section the stimulation of the nerve is sometimes followed by an increased effect. (See also Chapter VIII., Section 9, B., p. 395.) Since the section has cut off at least some channels of communication between the lower and upper parts of the cord, and presumably, therefore, has blocked the paths of some, even though few, nerve impulses, such a rise must be attributed to the greater intensity of the effect evoked in the remaining channels, whether nerve fibres or nerve cells, and the cord must therefore be considered to be hyperexcitable.

This alteration in excitability is probably associated with the phenomenon of hyperæsthesia observed by Fodera and Schiff to follow operative interfence with the

posterior columns. That it affects the cord on the side of the lesion is probable from the results just given, but the direct proof is wanting since the increased intensity of the effect is masked by the large diminution caused by the severance of the direct tract in the posterior column of the same side. There is, however, no such severance in the case of the opposite side, and the increased excitability is plainly seen as evidenced by the cases marked with an asterisk, in which the section was followed by actual increase in the cord effect. Whatever may be the meaning of this it undoubtedly is a most important factor to be taken into consideration in all experiments the general plan of which consists in first causing definite lesions, and then examining the influence of such. It will be obvious too, that in proportion as the anæsthetic is removed so much the more marked must this change in excitability become. In the experiment upon conduction already referred to, made by MIESCHER, in which the reflex effect on the blood pressure was taken as the index of the passage of afferent impulses through a block in the cord, any change of this kind could not be allowed for as owing to the curarisation of the animal, the observation of concomitant reflex movements was impossible. We venture to think that the increased effect obtained by MIESCHER on the side of the complete section in his division of every part of the cord except one lateral column, and taken by him to mean that the afferent fibres crossed into the lateral of the opposite side, was due to some such increased excitability in the lower fragment of cord on the side of the main lesion, the fibres of the lateral tract connecting this fragment with that above as internuncial fibres.

It is obviously impossible to put this factor completely out of court. The cord effect with which we are dealing is a measure at once of the intensity and the number of all transmitted excitatory processes, and the influence of any particular section can therefore only be judged of by taking the average of all the readings, high and low. It might be thought that by pushing the anæsthesia and by decreasing the strength of the stimulus the effect would always become uncomplicated. Although anæsthesia lessens the chance of its occurrence it would appear that this increase in the cord effect will sometimes occur even under these conditions; and it is then evidently dependent upon the character of the particular preparation used. Its presence or absence in these cases may, however, be not merely due to the idiosyncracy of the animal, but to minute differences in the extent of the lesion in certain instances.

The general result of experiments on four Cats and two Monkeys is as follows :—

EFFECT of Section of Posterior Column at the 10th to the 12th Dorsal Vertebra on the Opposite Side to the Nerve Excited.

	Cord observed at	Nerve excited before section.		Nerve excited after section.	
Cat (196)	10th dorsal	105 128 107	111		52
Cat (250)	8th dorsal		78		87*
Cat (377)	9th dorsal		78 125		90* 91
Cat (349)	9th dorsal		182	121 180	150
Total . . .	. . . . .		574		470
Ratio 100 to 81					

	Cord observed at	Nerve excited before section.	Nerve excited after section.
Monkey (281) . .	8th dorsal	155 230 250	150 170 199
Monkey	7th dorsal	65 82 96	105* 87* 120*
Total . . .	. . . . .	878	831
Ratio 100 to 94			

From these results it is seen that the cord effect is reduced by the section, and that this reduction in the observed cases was more marked in the Cat than in the Monkey. If we take the two sets of experiments together, as in the previous results of the division of the posterior column of the same side, then the reduction is found to be from 100 to 87, that is, 13 per cent.

This evidence therefore points to a crossing of effects from one side of the cord to the other as probable, such crossing and the ultimate conveyance of the impulses being more or less bound up with the posterior column on the opposite side to the stimulated nerve, to the extent of 13 per cent. in the animals we have as yet examined.

D. *Previous Section of Posterior Columns some time Previous to Observation.*

In one Cat (251) we divided the posterior columns at the level of the 10th dorsal vertebra four weeks before the experiments. When the animal (Cat) was examined it was noticed that the water test showed diminished sensibility in both hind feet, since the animal could be placed with its hind paws in water without exhibiting any movements of withdrawal. There were, however, vague symptoms that the two sides were not equal in the degree of sensibility they still possessed. This inequality showed itself in the knee jerks, the left being much feebler than the right. On placing the animal under ether, however, the left knee jerk was found to be then very much exaggerated, and the left hind limb was easily sent into a condition of clonic spasm.

The animal was first experimented upon by exposing and exciting the cord, and observing the changes in the nerves; the result of this experiment will be given in Chapter X. It was then used for the present series of experiments, the cord being originally divided at the 5th dorsal vertebra, and the upper end of the lower fragment prepared for galvanometric observation at about the 7th dorsal vertebra.

The left sciatic, when excited, with a minimal and a stronger stimulation, evoked effects of 10 and 20; the right, when similarly excited, evoked cord effects of 8 and 70.

The cord, after the death of the animal, was examined histologically, when it was found that the section had not been complete on the right side, a good many fibres having been left intact. On the left side it was complete, and at the level of the 7th dorsal, on microscopical examination, a sickle-shaped patch of degeneration could be seen in the postero-external column on each side, that on the left being very well marked, whilst that on the right was small. The same difference between the degeneration on the two sides could be seen at the level of the 4th cervical, where the degenerated area occupied, on the left side, a conspicuous portion in the middle third of the posterior median column. The discrepancy between the effects obtained between the two nerves is thus cleared up by the minute examination of the extent of the lesion. It furnishes striking evidence of the accuracy with which the electrical method can gauge the integrity of through tracts of fibres, but brings out a disadvantage, namely, that it involves the death of the animal; hence, when lesions, &c., are made *at the time* of the experiment, it is impossible to be perfectly certain of their extent, since the degeneration method, which alone would give absolute indications, cannot then be used.

Section 8.—Influence of Section of the Lateral Column.

Of the remaining columns in the cord, the lateral and anterior, it is only the former which appear to bear any relation to the production of the electrical effect in the

cord when the sciatic nerve is excited. This is shown by the fact that the cord effect is in no way modified by an interruption in the anterior columns which involves their complete severance, caused by a section between the entering nerve and the observed region. Such a section is most easily made in the isolated fragment of cord near its central attachment, since this portion is raised from its bed. This is in strict accordance with the fact alluded to in Chapter VIII., that excitation of the one end of the anterior column evokes no electrical effects in a distant portion of the cord.

It is otherwise with the lateral columns which have distinct relations with electrical effects in the cord, since, as shown in Chapter VIII., their stimulation evokes marked cord effects. It does not follow, however, that this relation is one which comprises the afferent nerves, for we know that the lateral column contains the main path for the efferent cord tracts, as is shown by the results of cortical excitation, as set forth in Chapter V., &c. The conclusion at which so many observers have arrived, that the main afferent path, whether crossed or uncrossed, is situated in the lateral column, is clearly not substantiated by any evidence offered by the employment of the present method, since the integrity of the two posterior columns is evidently essential for the production of at least 70 per cent. of the total effect. We shall see that the extent to which the two lateral columns are related to the afferent effect is small, being approximately only a fourth part of this amount, and that this is almost entirely confined to the lateral column on the same side as the afferent nerves excited. The results may be best displayed as follows :—

A. *Effect of Section of the Lateral Column on the same side as the Nerve Excited.*

The following experiments made upon four Cats show that the lateral column of the same side as the excited nerve, if divided, reduces the cord electrical effect evoked by excitation of the nerve to an extent the average of which is 20 per cent., that is, from 100 to 80.

Section of Lateral Column on the same Side as the Nerve Stimulated.

	Cord observed in region of	Effect before section.	Section at	Effect after section.
Cat (196) .	10th dorsal vertebra .	105	1st lumbar	115*
Cat (327) .	9th „ „ .	105	1st lumbar	76
		132		83
Cat (346) .	8th „ „ .	90	1st lumbar	60
		110		105
		542		439
	Ratio 100 to 80.			

The inference is that the integrity of the lateral column of the same side is connected with 20 per cent. of the cord effect. Additional ground for this conclusion is afforded by the opposite sectional method practised after the manner of Miescher and Woroschiloff, which, excluding the lateral column, divides everything else; the knife being placed perpendicularly through the cord from dorsal to ventral surface at the junction of the posterior and lateral columns, and then the cut made obliquely inwards towards the centre, and continued so as to come out on the opposite side. All the structures, with the exception of one lateral column, and the contiguous portion of the lateral horn are thereby severed. In some instances this operation was done piecemeal, first one and then another structure being divided.

The result of such severance of both posterior and one lateral column is to show that an electrical effect in the cord can still be obtained by stimulating the nerve on the same side as the uninjured lateral column. Its amount, as compared with the total change obtained before the section, is, however, greatly reduced, as is shown in the following Table, comprising experiments made on five Cats.

* It will be noted that in Cat 196 there ensued an increased effect after the section due to a rise in excitability.

Section of both Posterior Columns and Lateral on opposite Side to Nerve.

		Effect before section.	Intensity of stimulus.	Effect after section.
(195) Cat .	. . . . .	210	4000	6
(196) Cat .	. . . . .	86	4000	8
(256) Cat .	. . . . .	78	1000	23
(327) Cat .	9th dorsal vertebra . .	142	1000	35
(344) Cat .	8th „ „ . .	6	500	28
		122	1000	35
		152	2000	27
		856		162
	Ratio 100 to 19.			

That is to say, this remaining effect represents 19/100 of the whole. This result tallies with that obtained with the other method, which showed that the section of this lateral only reduced the effect by about 20 per cent. This reduction in the cord electrical change is thus a reduction in the number or intensity of the afferent impulses which pass up the cord when the nerve is excited. Hence, as far as the method goes, it would appear that the lateral column on the side of the stimulated nerve furnishes a path, whether internuncial or not, we cannot say, but, at any rate, an indirect one for the transmission of 20 per cent. of the nerve impulses.

B. *Effect of Section of the Lateral Column on the opposite side to the Nerve Excited.*

The contradiction which exists between the results of the present research and the interpretation given to their experiments by Miescher and Woroschiloff is brought into the strongest prominence by the consideration of the present group of results. If the interpretation of these physiologists is warranted by their data, and is of general application, then we should expect that the integrity or otherwise of the lateral column opposite the entry of a stimulated nerve would have the preponderating influence upon the passage of those nerve impulses which have entered the cord by the nerve, and consequently upon the amount of the electrical change in the observed portion of cord. We have, however, already accounted for 95 per cent. of the effect by showing that the amount is dependent upon the integrity of the other columns, and this fact alone is sufficient to show what a small share the integrity of the opposite lateral column has in providing channels for the conduction of ascending impulses.

We have made experiments upon five different animals, the results being separated into those in which the lateral column was divided on the opposite side to the nerve, and those in which all structures, except the opposite lateral column, were cut

INFLUENCE of Section of the Lateral Column on the opposite Side to the Excited Nerve on the Cord Effect.

	Cord divided and observed at	Effect before section.	Stimulus.	Effect after section.
(196) Cat .	10th dorsal vertebra .	86	4000	100
(327) Cat .	9th ,, ,, .	82	500	78
		142	1000	125
(346) Cat .	9th ,, ,, .	110	1000	63
		110	2000	112
		530		478
	Ratio 100 to 90.			

It will be noticed that in only one case (346) was there any marked reduction, and that this did not occur when the intensity of the stimulus was increased. Instead of reducing the effect the section in two cases increased it. The average reduction of 10 per cent. is probably too high, owing to some unknown factor being present to cause the exceptional low reading. This presumption is rendered more probable by the next set of results, the converse experiments.

SECTION of all Columns except Lateral on Opposite Side to Excited Nerve.

	Cord divided and observed at	Effect before section.	Stimulus.	Effect after section.
(196) Cat .	10th dorsal vertebra .	105	4000	10
(256) Cat .	8th ,, ,, .	90	1000	0
(327) Cat .	9th ,, ,, .	142	1000	5
		105	500	5
(344) Cat .	8th ,, ,, .	74	500	3
		93	1000	15
		135	2000	3
		734		41
	Ratio 100 to 6.			

These results show that at any rate under the conditions which were present in these experiments, those, namely, of moderate narcosis, the lateral column of the cord opposite to the nerve excited can transmit only 6 per cent. of the nerve impulses which produce the electrical change in the cord when all the other structures are divided. To what extent it can act as a bridge when the ether is removed, as in MIESCHER

and Woroschiloff's experiment we have not yet had an opportunity of observing. The experiments would have to be done under curare to avoid the dragging on the cord by the convulsive movements of the animal and without anæsthesia, analgesia being provided for by section of the peduncles. They are, therefore, of a very special kind, and involve much consideration before embarking upon them.

Section 9.—Summary.

We will now sum up the results of the foregoing experiments, pointing out at the same time the deficiencies as well as the advantages of the method employed.

I. Electrical changes in the lower dorsal region of the cord are readily evoked by exeitation of the sciatic nerve, or the posterior roots of the lumbar plexus.

II. These changes are dependent in the anæsthetised animal on the integrity of particular columns of nerve fibres stretching between the region observed and the neighbourhood of the entering nerves.

III. The total amount of electrical change is an indication of the amount of nerve energy flowing up the cord from the stimulated nerve. If the total amount be represented as 100, then the following numbers represent approximately the amount which flows up each column and which is thus interrupted by its section :—

Posterior column same side	60
Posterior column opposite side	15
Lateral column same side	20
Lateral column opposite side	5

IV. The flow of nerve energy up the cord is thus mainly unilateral, 80 per cent. being transmitted in the channels on the same side as the entering nerve.

V. The comparatively small amount of nerve energy which crosses into the opposite side of the cord is almost entirely localised in the posterior column of that side.

These conclusions are, it will be observed, simply confirmatory of those already indicated in the preceding chapter, in which it was pointed out that no electrical evidence existed of any crossing of ascending impulses in the cord from the fibres in one lateral column to those of other columns; and that the peculiarity of the ascending impulses in the cord is (*a*) the direct path they take up the posterior column of the same side, and (*b*) the indirect path by spread from the posterior column, first into the lateral column of its own side, and then across into the posterior column of the opposite side.

Finally, our experiments do not show the path taken by sensory impulses; it is possible, though hardly conceivable, that these are essentially different in quality to the ones we have been studying. All we can say is that when nerve impulses are evoked in the afferent fibres of the sciatic nerve, and proceeding up these reach the cord, they apparently find several paths open to them. These paths, however,

are either not equally numerous, or are not equally easy of passage; the posterior column of the same side offers special facilities for the passage of the impulses, the lateral column of the same side offers facilities greater than the posterior column of the opposite side, but both, whilst far inferior in this respect to the posterior column of the same side, are far superior to the remaining lateral column of the opposite side. This last, at least in the narcotised animal, offers practically no facilities for such passage.

It is, perhaps, unnecessary to draw attention to the circumstance that the above results are only verified in the case of the lower dorsal region of the cord in the Cat, and to some extent in the Monkey.

The principal deficiencies of the present method have been indicated in this and previous chapters, but may now be summarised. They are connected—

(*a.*) With the character of the nerve impulses, which, being due to electrical excitation, are more intense, and possibly different in quality, to those which are generated in peripheral sensory end organs.

(*b.*) With the necessity of insulating the observed portion of cord, to ensure the observation of localised effects in it, this being accomplished by a severe operation which entails the death of the animal at the close of the experiments.

(*c.*) With the limited anatomical scope of the method as at present used, the highest point which we have reached being the mid-dorsal region. The shock of the exposure above this has rendered our experiments, carried out higher than this, unsuccessful.

The chief merits of the method are—

(*a.*) That the changes investigated are the electrical excitatory processes in the cord itself severed from the encephalon, and are free, therefore, from admixture with cerebral effects, and are independent of the reflected outcome of such effects in the muscles.

(*b.*) That the changes are so definite as to admit of comparison as to their quantity, and thus of a quantitative estimate of the nerve energy transmitted in the cord under different conditions.

(*c.*) That this quantitative character of the results enables a comparison to be made of the effects of nerve energy which are dependent respectively on the integrity of the different parts of the cord.

The conclusions to which we have thus arrived will receive additional confirmation from the results of experiments in which the impulses in the nerves are made the subject of investigation by the electrical method, such impulses being aroused by excitation of the different columns in the cord.

These will be detailed in the next chapter, at the end of which a general review of the whole question of conduction in the cord, as elucidated by our method, will be given.

CHAPTER X.—ELECTRICAL CHANGES IN THE NERVES FOLLOWING EXCITATION OF THE SPINAL CORD.

Section 1.—Introductory.
Section 2.—Plan of experiments and preliminary observations.
Section 3.—Electrical effects in sciatic nerve following excitation of different columns of the cord.
Section 4.—Electrical effects in afferent nerves following excitation of the cord:
(1.) Posterior roots.
(2.) Sciatic nerve after section of anterior roots.
Section 5.—Electrical effects in efferent nerves following excitation of the cord.
Section 6.—Influence upon the effects in the nerve of intervening sections of the cord.
A. Influence of hemisection.
B. Influence of section of the posterior column on the same side.
C. Influence of section of the posterior column on the opposite side.
D. Influence of section of both columns.
E. Influence of section of the lateral columns.
Section 7.—Summary and conclusions.

Section 1.—Introductory.

In the foregoing chapter the results have been given of the observation of a new index of cord activity, that of noting the accompanying electrical effects when the afferent nerves were excited together with the influence upon these of a series of intervening sections.

It will be seen that the plan of the whole of that research was upon the lines of previous investigations, except as regards the index employed; in the experiments to be detailed in this section both the method and plan of experiment are entirely novel, since conclusions can only be arrived at by the evidence afforded by the electrical effects as indicative of the presence or absence of excitatory changes. The novelty consists in this, that we are able to detect excitatory electrical effects in the issuing nerves when the cord is stimulated; not merely in the nerves themselves, but in their roots. Now as far as the efferent motor roots and motor portion of the mixed nerves are concerned, the method whilst giving us valuable information has obvious relations with the data which have already been obtained by the graphic method of recording the muscular contractions; but as far as the afferent sensory nerves are concerned, it introduces us to previously unknown relationships, for there is no indication other than an electrical one at present known, which can detect the passage of nerve impulses from the cord into afferent tracts, since such passage is opposed in direction to that of the normal transmission as usually understood. It has been already stated that one of the most valuable results of the discovery of the excitatory electrical change was that set forth by du Bois-Reymond, as proving the propagation of excitatory effects in both directions along a continuous tract of either afferent or efferent nerve fibres, this being evidenced by the presence of the electrical change at

both ends of a nerve when the middle portion is stimulated. We have seen that similar evidence in the case of the nerve fibres in the cord shows that in them also the effect is propagated from the stimulated region indifferently either towards the centre or the periphery, and it follows from the combination of these two, that if any fibres in a nerve are directly continuous with those in the cord, the excitatory changes following stimulation of these must be propagated along the whole length of the continuous strand and may thus travel out into the fibres of the nerve. Direct continuity has been shown to exist by the degeneration method between the fibres of the posterior root and those of certain portions of the posterior columns, hence it is not surprising that the stimulation of the posterior columns in the cord should cause electrical changes in the posterior root due to the arrival in the fibres of this structure of excitatory processes transmitted from the cord down tracts which, owing to their terminal relations, are usually believed to be solely ascending ones. There is nothing to warrant the belief that these descending impulses in afferent nerves, evoked by excitation of the columns in the spinal cord, are in themselves different from those which are evoked by similar methods of excitation when applied to the peripheral parts of the afferent nerves, and which are propagated in the natural direction, since it seems to be fundamental as regards nerve conduction that fibres can conduct equally in either direction.

The fact that in one group of nerve fibres (afferent) the starting platforms are at the peripheral end, and the receiving termini at the central, whilst in the other (efferent) the positions are reversed, and that, in consequence, what are called normal nerve impulses proceed in the afferent direction in the one group and in the efferent in the other, apparently has not, physiologically or structurally, altered the fibres (polarised them in any way) so as to make conduction in the one direction more difficult than in the other. As far, then, as the directly continuous afferent fibres are concerned, there is no difficulty either in obtaining electrical results in the posterior roots on exciting their direct prolongations in the cord, or in interpreting these as indicative of the passage of nerve impulses.

A much more complicated condition must, however, be now referred to, that, namely, of the nerve fibres which are only indirectly continuous with others in the cord, there being interposed in their path corpuscular elements and unknown channels.

The simplest of these are the efferent (motor) nerves, and it has already been stated that, as regards these, Chapter IX., Section 2, the corpuscular connection is of such a character that, whilst allowing the passage of impulses from the cord to the nerves, it appears to completely block the passage of impulses from the nerves into the cord. (See also Chapter XI., Section 2 (1).) The stimulation of a mixed nerve (the posterior roots being divided) or an anterior root thus evokes impulses which travel up and break upon the shore of the nerve corpuscles, and either remain on

their peripheral side, or issue in such broken and disorderly array that their character is completely lost, and all evidence of their presence disappears.

To what extent is this true of the afferent root fibres? The answer to this question is one which can only be appreciated when the results of the experiments of both this chapter and the succeeding one, upon the reflex functions of the cord, have been analysed; but it may be well here to state at once that there is no evidence of such pronounced block to impulses which may be caused to descend the indirect paths by which the posterior root fibres are brought into connection with the cord.

The difficulties of interpreting the experimental results are increased by the gap which exists in our anatomical knowledge as to the connection between these indirect afferent fibres and the cord. This connection is one upon which the degeneration method throws but little light, although it would appear probable from the trophic changes observed, and from morphological considerations, that there are cells in the posterior horn, and possibly in CLARKE'S column, which are connected with fibres in the posterior roots (MOTT). The recent researches of KÖLLIKER seem to indicate that the termination of some of these indirect fibres in the cord is largely that of a fine plexus with free ends.

Although the central connections of the fibres are as yet to a great extent unknown, yet the description indirect as distinguished from direct is warranted by its wide-spread use. It is advisable, however, to emphasise what the term indirect as used by us in the present case is understood to connote.

It is descriptive of all afferent fibres in the cord, which may be supposed to be connected with those of the posterior root, but which do not show any of the degenerative and developmental differences which stamp some fibres (posterior median) as being in direct continuity with the root. There is, however, nothing in itself to show that this term indirect is a strictly logical one; since the same line of argument might be applied to those fibres which pass through the ganglion on the posterior root, with regard to which the degeneration method furnishes no evidence of direct continuity (JOSEPH).

Impulses are conducted through the ganglion in either direction (DU BOIS-REYMOND), and apparently without any modification in their time relations (EXNER) if we may suppose that this is due to the fact that, apart from the few fibres which appear not to come into relation with cells at all, the relationship of the majority of fibres to the ganglion cells is of the T-piece kind, as shown by RANVIER, in which case the cell does not interrupt the continuity of the connected fibre. There is no reason why some such sort of bypath (GOLGI) may not be the basis of the connection of the fibres with the corpuscular elements in the spinal cord, as it is in certain parts of the cerebrum (FLECHSIG).

There are, therefore, no anatomical data which are necessarily implied in the term indirect as applied to these fibres, beyond the fact that such fibres come into

connection in some way with some element in the cord, which serves as a common centre both for nutrition and for growth.

The researches on the conduction of afferent impulses from the nerves into the cord detailed in the preceding chapter, as well as our other experimental investigations, show that such paths undoubtedly exist. The present experiments will prove that these, although indirect, are capable of conducting impulses from the centre towards the periphery; the only distinction between the indirect and the direct path, in this respect, being the greater intensity of the stimulus necessary to produce the evidence of such effects in the case of the former, and the comparatively small amount of the nerve energy which can be thus evoked, through the indirect path, in the afferent nerves. In other words, the direct path is that of least resistance to impulses when these pass backwards from the cord into the afferent nerves.

We now pass to the consideration of the detailed plan of the experiments as a necessary prelude to the analysis of the results.

Section 2.—Plan of Experiments and Preliminary Observations.

Our first experiments upon the nerve effects following cord excitation were crude in design. They were made by first dividing the cord in the dorsal region, then preparing one sciatic nerve in the back of the thigh, ligaturing it, dividing it, and connecting its central end and the adjoining longitudinal surface by means of cable electrodes with the galvanometer, and finally stimulating the cord by means of needles which pierced it and acted as electrodes to the secondary coil of the inductorium. We satisfied ourselves in this way that the excitation of the cord was followed by excitatory electrical changes in the nerve, and then proceeded to more methodical experiments. In these the cord was carefully exposed by dissection and a piece removed, so that the cross section of its surface could be easily seen. The various cut ends of the columns were then excited as desired by a series of interrupted induction currents (Helmholtz side-wire) for a period which was controlled by the revolving mercurial key, and was carefully kept of the same duration during any set of observations. A pair of well-insulated fine platinum-pointed electrodes were used for the stimulating current, these being applied to the particular region of the cross section it was desired to excite, in the manner and under all the precautions already described in Chapters III. and VIII. The sciatic nerve when raised in air and connected with the galvanometer displayed the usual resting electromotive difference between its two points of contact. This difference has been referred to at length in Chapter IV. and was compensated in all cases. On exciting the cord for five seconds an electrical effect was produced in the nerve which was always opposed in direction to the resting current, and which passed away on the cessation of the stimulus. The amount of the deflection was in most cases considerably less than was obtained by applying the same stimulus (unaltered in intensity and duration)

to the trunk of the nerve. It was notably affected by several conditions, of which the most important are those affecting the state of the animal and those connected with the intensity of the stimulus. The influence of these two conditions demands closer examination.

The state of the animal has the greatest influence on the amount of the change. To take the most powerful factor first, the systemic death of the animal, this is at once shown in the diminishing size of the effect, until, in about ten minutes, no electrical change can be evoked in the nerve when the cord is excited.

The following experiment may be quoted in illustration of this point; it is one in which the posterior root instead of the nerve was observed.

The cord of a Cat was divided at the 10th dorsal and the cauda equina exposed. The 7th lumbar posterior root on the left side was then ligatured and divided near the ganglion, raised in air and its central end and surface connected with the galvanometric electrodes.

Excitation for five seconds of a given tract in the cord (the left posterior column) evoked an electrical change indicated by a galvanometric effect of 253. The animal suddenly died from collapse, the heart failing, and the experiment was then repeated about four minutes after death, when the deflection was found to be less, viz., 165.

The time of this observation was 12.1. A series of such observations were then made as follows:—

Time.	Deflection.
12. 1	165
12. 2	142
12. 3	139
12. 5	75
12. 7	50
12.10	8
12.12	nil

Excitation of the root itself still evoked considerable effects at 12.15. We have often had the opportunity of noting that the nerve electrical effect when evoked by excitation of the cord, disappears on death earlier than when evoked by excitation of the nerve trunk. This we imagine to be due partly to the circumstance already mentioned that the latter excitation produces normally a more marked effect than the former, and partly to the changes in excitability which, in accordance with the Ritter-Valli law, proceed from the centre towards the peripheral attachment of a nerve.

A more important influence than this of death, since it is one present throughout all the experiments, is that dependent upon the varying degree of anæsthesia. There are many experiments which furnish illustrations of this point. A stimulus of the same character, intensity, and duration, applied to the same region of the cord, evokes

now a larger and now a smaller effect, dependent upon marked lessening and deepening of the narcosis. The importance of bearing this in mind is sufficiently obvious; it is, however, capable of control, since the character of the movements awakened by the stimulus furnishes a fair index of the condition of anæsthesia, and was in all cases closely observed.

Finally, the influence of temperature is one to which attention has already been directed in Chapter III., and although the necessity of keeping the exposed cord covered with warm sponges, except during the actual stimulation, has been already dwelt upon, it may be insisted on again at this juncture.

Alterations in the duration and intensity of the stimulus modify the effect; the longer the duration and the greater the intensity, the more pronounced is the nerve change. The modifications are so marked, that in analysing and comparing the quantitative value of the nerve effects obtained by stimulation of different regions of the cord, it will be necessary to divide the indicative galvanometric deflections into two classes, as evoked by "minimal" and maximal stimuli respectively. It will be understood, however, that a rigid separation is impossible, there being every grade between an undoubtedly "minimal" effect with no accompanying reflex movements and an undoubtedly maximal effect with vigorous movements.

The experiments were made upon twenty-one Cats and six Monkeys, and may be divided into four groups, the first three of which differ as regards the nerve fibres in which the electrical change was observed, the fourth differing as regards the condition of the cord, through the stimulation of which the nerve effect is evoked. We have, therefore, to consider in succession:—

The electrical effect in the mixed sciatic nerve;
,, ,, afferent nerve roots;
,, ,, efferent nerve roots;
The modifications produced by intervening section of tracts in the cord.

Each group will form the subject of a succeeding section.

Section 3.—The Electrical Effects in the Sciatic Nerve following Excitation of the Different Columns of the Cord.

The experiments upon this subject will be best displayed by first selecting and describing the results of a particular experiment in the Cat and Monkey respectively, and then giving a table which will show the averages of all the comparable observations.

The spinal cord was exposed and divided in an anæsthetised Cat (331), at a level between the 10th and 11th dorsal vertebræ; both the sciatic nerves were then carefully exposed, ligatured in the lower part of the thigh, and divided on the peripheral side of the ligature. They were then freed from their attachments and raised in the

air by the ligature. A separate pair of non-polarisable electrodes was placed in connection with the cross section and the surface respectively of each nerve. A piece of cord 1 centim. long was now removed from the upper end of the lower fragment of the cord, thus exposing a fresh cross section of all the columns.

The left sciatic nerve showed a resting electrical difference between the surface and cross section, which was balanced by a difference of ·01 Daniell; the right nerve showed a rather less marked difference balanced by ·008 Daniell.

Each pair of nerve contacts was alternately connected with the galvanometer, a Pohl's reverser without cross wires being used to switch either set of contacts into connection. The following deflections, opposed in direction to the resting difference, were obtained from the nerve when the cut ends of the various columns designated below were excited for 5 seconds :—

Left Nerve connected.

Strength of stimulus.	Region excited.	Effect.
Secondary coil. 500	Left posterior column . . .	140
	Left lateral ,, . . .	Nil
	Right posterior ,, . . .	15
	Right lateral ,, . . .	Nil
	Anterior columns	Nil

Right Nerve connected.

Strength of stimulus.	Region excited.	Effect.
Secondary coil. 500	Left posterior column . . .	5
	Left lateral ,, . . .	Nil
	Right posterior ,, . . .	65
	Right lateral ,, . . .	Nil
	Anterior columns	Nil

The intensity of the stimulus was now doubled.

Left Nerve connected.

Strength of stimulus.	Region excited.	Effect.
Secondary coil. 1000	Left posterior column . . .	190
	Left lateral ,, . . .	5
	Right posterior ,, . . .	30
	Right lateral ,, . . .	Nil.

RIGHT Nerve connected.

Strength of stimulus.	Region excited.	Effect.
Secondary coil. 1000	Left posterior column . . .	5
	Left lateral ,, . . .	Nil
	Right posterior ,, . . .	132
	Right lateral ,, . . .	Nil
	Anterior columns	Nil

Intensity of stimulus again doubled.

LEFT Nerve connected.

Strength of stimulus.	Region excited.	Effect.
Secondary coil. 2000	Left posterior column . . .	240
	Left lateral ,, . . .	16
	Right posterior ,, . . .	40
	Right lateral ,, . . .	Nil
	Anterior columns	Nil

RIGHT Nerve connected.

Strength of stimulus.	Region excited.	Effect.
Secondary coil. 2000	Left posterior column . . .	15
	Left lateral ,, . . .	Nil
	Right posterior ,, . . .	172
	Right lateral ,, . . .	5
	Anterior columns	Nil

The above experiment shows plainly that, with a weak stimulus, an effect is only produced in the nerve by stimulating the posterior columns, and that this effect is very marked when the directly continuous fibres in the posterior column of the same side as the observed nerve are excited, and is small when the fibres of the posterior column of the opposite side are excited. A very small effect is produced by stimulating the lateral columns until the stimulus is strong, and even then an appreciable effect is obtained only from the excitation of the lateral on the same side as the nerve.

A similar experiment may now be quoted in detail upon the Monkey (333) (*Macacus sinicus*). The cord was divided in the anæsthetised animal at the 10th dorsal vertebra, so that the cut ends of the various columns could be excited as in

the previous experiment. Both nerves were then prepared and connected alternately with the galvanometer in the manner already described. The excitatory electrical effects in each nerve following the stimulation of the different columns of the cord were observed with different intensities of stimulus, and the results, which are analogous to those obtained in the Cat, are shown in the following Table. The left nerve was found to be less excitable than the right, but the resting difference of both was ·005 D.

LEFT Nerve connected.

Intensity of stimulus.	Region of cord excited at cross section.	Deflection of galvanometer.
2000	Left posterior column . . .	14
	Left lateral ,, . . .	Nil
	Right posterior ,, . . .	3
	Right lateral ,, . . .	Nil

RIGHT Nerve connected.

Intensity of stimulus.	Region of cord excited at cross section.	Deflection of galvanometer.
2000	Left posterior column . . .	12
	Left lateral ,, . . .	Nil
	Right posterior ,, . . .	68
	Right lateral ,, . . .	10

Intensity of stimulus doubled.

LEFT Nerve connected.

Intensity of stimulus.	Region of cord excited at cross section.	Deflection of galvanometer.
4000	Left posterior column . . .	106
	Left lateral ,, . . .	25
	Right posterior ,, . .	39
	Right lateral ,, . . .	Nil
	Anterior columns	Nil

RIGHT Nerve connected.

Intensity of stimulus.	Region of cord excited at cross section.	Deflection of galvanometer.
4000	Left posterior column . . .	52
	Left lateral ,, . . .	Trace
	Right posterior ,, . . .	112
	Right lateral ,, . . .	6
	Anterior columns	Nil

The effect in the mixed nerve of the Monkey is thus shown to be most strongly evoked when the excitation is that of the posterior column on the same side as the observed nerve. This preponderance over those effects which are evoked in a minor degree from stimulation of the lateral of the same side and the posterior of the opposite side is very marked when the stimulus is minimal.

The two experiments thus quoted form two in a series similarly made upon six Cats and five Monkeys, and the average results of all galvanometric deflections obtained in these form the most reliable data from which to draw any conclusions as to the relations between the amount of electrical change in the mixed nerve and the special regions of the cord which were stimulated. We must, however, again discriminate between effects evoked by stimuli of only just sufficient intensity to ensure their presence, which we term *minimal* (*i.e.*, 500 to 1000), and those which more strongly arouse the region excited, *maximal* (*i.e.*, 2000, occasionally 4000); hence, for every column excited, we have the result of a minimal and a maximal stimulus.

Moreover, it is obviously useless to designate which nerve is connected with the galvanometer, if we place together—

A. All effects evoked by excitation of the posterior column which is on the same side as the nerve.

B. All effects due to excitation of the posterior column on the opposite side to the nerve.

C. Those due to stimulation of the lateral column on the same side.

D. Those due to stimulation of the lateral column on the opposite side.

Any alterations in the stimulation as to intensity and duration necessary in different animals do not affect the value of any comparison between the quantitative results of the members of each different group, since the stimulus was always the same during any one set of observations, and each set included stimulation in regular succession of all the different columns indicated. The total result of such observations in the Cat is as follows:—

CAT.

Animal.	Cord divided at	Effect in sciatic nerve following							
		A. Excitation of posterior column of same side.		B. Excitation of posterior column of opposite side.		C. Excitation of lateral column of same side.		D. Excitation of lateral column of opposite side.	
		Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.
Cat (254) . .	8th dorsal . .		85		20				0
			80		8				0
			82		18		12		0
Cat (265) . .	11th dorsal . .	36	86	0	32	0	7	0	0
				0		0		0	
Cat (311) . .	8th dorsal . .	49	130		20				
			152		26				
			108		36				0
Cat (329) . .	9th dorsal . .	50	85	5	25	0	10	0	0
		28	89	5	22		9		
Cat (363) . .	9th dorsal . .	42	122	8	10	0	15	0	
		65	145	5	28	0	10	0	
			138		28				
Cat (331) . .	10th dorsal . .	65	140	5	15	0		0	
			190		30		5		0
			132		5				
			172		15		5		0
			240		40		16		0
Aggregate sum		335	2178	28	378	0	89	0	0
Average		48	128	6	22	0	10	0	0

From this it will be seen that with the minimal stimulus effects were obtained only on exciting the posterior columns ; that the effect, due to excitation of the posterior column on the same side as the nerve, was eight times as large as that due to excitation of the posterior column on the opposite side ; and that no effect was produced by stimulation of either lateral column. With a stronger stimulus, it is seen that the effect evoked from the posterior column of the same side was five times as large as that obtained from the posterior of the opposite side, and further an effect was obtained from the excitation of the lateral column on the same side as the nerve.

Turning now to the Monkey, the results similarly grouped, are as follows :—

MONKEY.

Animal.	Cord divided at	Effect in sciatic nerve following							
		Excitation of posterior column of same side.		Excitation of posterior column of opposite side.		Excitation of lateral column of same side.		Excitation of lateral column of opposite side.	
		Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.
Monkey (270) .	8th dorsal . .	59		0		0		0	
		40	70	0	42	0	6	0	0
Monkey (280) .	7th dorsal . .		190		10		2		
			192		2		2		
			135		33		80		0
Monkey (221) .	10th dorsal . .		98		26		45		8
			50		15		6		12
			57		24		40		2
			102		10		20		3
Monkey (333) .	10th dorsal . .	58	68	18	12	0	10	0	0
			106		37		25		0
			112		52		6		0
Monkey (368) .	10th dorsal . .	55		16		4		0	
		58		2		0		0	
			38		6		30		0
			37		14		9		5
			20		8		23		0
Aggregate sum		270	1275	36	287	4	304	0	30
Average		54	91	7	21	—	22	0	2·5

It will be seen that with "minimal" excitation the average effect obtained in the sciatic nerve of the Monkey by the excitation of the posterior column of the same side was nearly eight times as great as that of the posterior column of the opposite side. A small effect was obtained once after excitation of the lateral column of the same side, otherwise these results are in complete harmony with those in the Cat.

With the stronger stimulus the average effects following excitation of the two posterior columns have the relation of nearly five to one, the larger being due to that of the posterior of the same side; and, as in the Cat, a marked effect follows the excitation of the lateral of the same side, this being equal to that evoked by stimulation of the posterior column of the opposite side.

Finally, if all the results in both animals are blended and we compare both the average effect and the highest deflection obtained in response to excitation of each of the columns, the comparison shows the following results.

Average Nerve Effect produced by Cord Excitation (Cat and Monkey).

	Average.	Highest.
Posterior column, same side	80	192
„ „ opposite side	15	68
Lateral column, same side	9	80
„ „ opposite side	4	12
Total	110	

The sum of the average effects produced by all the columns is 110; of this the posterior column on the side of the nerve is capable of evoking about 73 per cent., the posterior column of the opposite side 15 per cent., the lateral column of the same side 9 per cent., and the lateral column of the opposite side 3 per cent.

There is a great similarity, at least as regards the relation of the crossed to the uncrossed side, between these different quantities and those which were referred to at the end of the nerve-to-cord experiments, detailed in Chapter IX. An exact similarity could not be expected, since we are dealing in the present case with mixed nerves, hence efferent as well as afferent fibres are the subject of observation.

The presence of impulses which may be supposed to emerge from the cord by the anterior roots might account for an increase in the effect evoked in the nerves, since the excitation of such columns as the posterior may awaken reflex discharges from the cord down the motor roots.

This explanation, however, cannot be applied to the effects evoked by excitation of the lateral column on the side of the nerve, since we see that the effect evoked by this column is smaller than that which the results of Chapter IX. would lead us to expect as probable from the indirect connections of its fibres with those of the posterior root only. There is no evidence of any accession of nerve impulses through this excitation, but rather of a resistance to the passage of impulses from the cord through the lateral indirect path into the fibres of the mixed nerve.

It is, however, essential to ascertain the amount of the effects in the afferent and efferent nerve tracts before proceeding to discuss in more detail what the above experiments seem to indicate as to the relations of the cord to its nerves.

Section 4.—The Electrical Effects in Afferent Nerves following Excitation of the Spinal Cord above their Point of Entry.

(1.) *The Posterior Roots.*

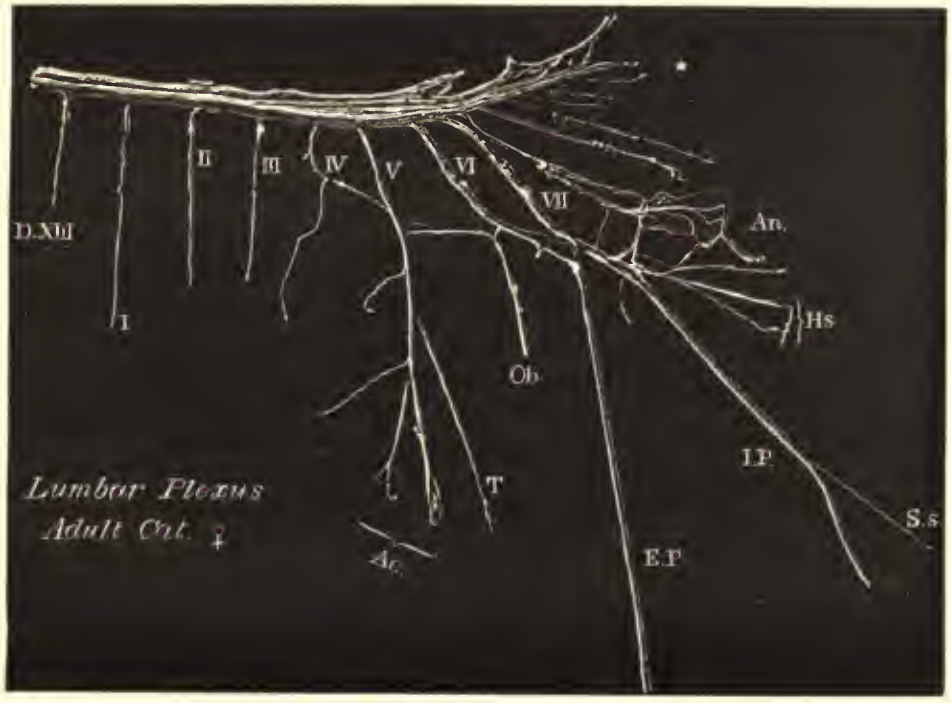
The simplest mode of obtaining the effects in afferent nerves is that of exposing a posterior root, dividing it near the ganglion and connecting its cut central end and

the surface immediately above with the galvanometer circuit in the manner described. The objections to this experiment consist in the great shock to the animal which the necessarily prolonged exposure of the roots necessitated by the procedure seems to cause, and in the fact that the posterior root does not hold out as long as the sciatic nerve, its excitability being more readily influenced by falling temperature, drying, &c.

We have however succeeded in three different animals (Cat) in obtaining a series of readings of the value of the root effect, the details of the experiments being as follows :—

In all three animals, the left 7th lumbar posterior root was selected, this being the largest of the posterior roots in the Cat which receives afferent fibres from the sciatic nerve, as shown in the accompanying reproduction of a photograph of the plexus. (See fig. 18.)

Fig. 18.



The cord was first exposed in the lower dorsal region and prepared for excitation at the level indicated in the table, and then the cauda equina, and thus the roots, laid bare. The 7th lumbar root was then exposed from origin to ganglion, ligatured near the ganglion and divided. It was raised in air by the ligature, and cables placed round its ligatured cut end and its surface 1 centim. above. The roots, as stated in Chapter IV., were remarkable in exhibiting a comparatively large resting electromotive difference between the surface and the cut section.

The different columns of the cord were then excited, first with "minimal" and then with maximal stimulation ; it was found that the electrical effect in the root resembled

that of the nerve in character, but owing to the difficulty of keeping the root protected, and at the same time insulated, the amount of the effect, and, presumably, the excitability of the root, declined, especially in one Cat (341); the results, therefore, are all modified by the fact, that as the "minimal" stimulus was applied first, the deflection caused by the excitatory electrical root change is much larger in the case of the "minimal" stimulus relatively to that of the "maximal" stimulus than would otherwise be the case.

The following table gives the results of the galvanometric observations; each deflection being produced by electrical changes in the nerve root, corresponding to the localised excitation, for five seconds, with the interrupted induction current of the sectional area of a special tract of the cord as indicated below.

EFFECT in Left 7th Lumbar Posterior Root.

Animal.	Cord excited at level of	Excitation of left posterior column.		Excitation of right posterior column.		Excitation of left lateral column.		Excitation of right lateral column.	
		Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.
Cat (341) . . .	12th dorsal .	190		9		0		0	
		135		6		0		0	
			110		32		0		0
			108		19		0		0
			90		50		0		0
			90		45		10		0
Cat (348) . . .	11th dorsal .	192		2		0		0	
		170		2		0		0	
			200		70		0		0
Cat (362) . . .	10th dorsal .	50		2		0		0	
			240		45		0		0
			253		15		0		0
Total sum		735	1091	21	276	0	10	0	0
Average		147	156	4	39	0	—	0	0

It is seen that with the minimal stimulus an effect is practically only evoked by excitation of the posterior column of the same side as the root; with a stimulus of greater intensity an effect is also obtained with stimulation of the posterior column of the opposite side, this being one-fourth the amount of that evoked by stimulation of the column of the same side. As regards the lateral columns, only once was any effect in the root obtained, and that was with stimulation of the column of the same side.

If it be remembered that the minimal effect is exaggerated in the case of the posterior columns by the fact that their stimulation coincided with the fresh condition of the root, it will be seen that as far as the relations between the effects due to

excitation of the two posterior columns are concerned, the above experiments give results which are fundamentally the same as those obtained in the mixed nerve. On the other hand, the lateral column effect is almost entirely wanting in these experiments. The alterations in the excitability of the posterior root itself may be to some extent responsible for this, and in any case should, if possible, be excluded. In order to carry out this exclusion, experiments were performed in which, whilst investigating the effect in the mixed sciatic nerve, the (motor) efferent paths were annulled by section of all the anterior roots of the lumbar plexus.

(2.) *Effects in the Sciatic Nerve after Section of Anterior Roots.*

This experiment we have performed on two animals (Cats), in each of which the cord was divided and exposed for excitation at the level of the 11th dorsal vertebra, and the left sciatic nerve prepared in the usual way for connection with the electrodes. The lower lumbar cord and the cauda equina were then exposed in each animal by opening the canal for about 5 centims. The anterior roots of the left 5th, 6th, and 7th lumbar, and 1st and 2nd sacral nerves, were cut within the canal. All other connections were then divided, so as to leave the left sciatic nerve in connection with the cord by the posterior roots only.

The excitation of the cord proceeded in the usual manner, but a "maximal" intensity of stimulus alone was employed, and the time of stimulation was 7 seconds.

EFFECT in Left Sciatic Nerve after Division of its Anterior Roots.

Animal.	Cord divided at	Excitation of left posterior column.	Excitation of left lateral column.	Excitation of right posterior column.	Excitation of right lateral column.
Cat (209). .	11th Dorsal	125 130 85 92	not observed 50 not observed ,,	9 35 15 not observed	0 0 not observed ,,
Sum.		432	50	59	0
Average		108	50	20	0

From these figures it will be seen that the effect evoked in the sciatic nerve by excitation of the posterior column on the same side was more than twice as large as that resulting from excitation of the posterior on the opposite side and more than four times as large as that due to the lateral on the same side.

In another animal the same anterior roots were divided, and in addition all the posterior roots on the left side and all nervous connections except the 7th lumbar posterior root, thus leaving the left sciatic nerve as a mere continuation of this

7th lumbar posterior root. Effects of 35 and 20 were obtained from excitation of the posterior column on the same side, and an effect of 10 with excitation of the posterior column of the opposite side; no effect followed the excitation of the laterals. This experiment is very difficult in execution, owing to the depressing effect which the severe character of the operation produces in the cord, both directly and indirectly, through shock to the animal. We have tried the experiment several times without success. As far as they go, the results of the second experiment would seem to indicate that the lateral column effect is not present when only one channel of influence, that of the 7th lumbar posterior root, is present, and this result is in accordance with the observations made upon the posterior root itself. It is not impossible that the results of the first experiments with the sciatic nerve given in Section 3, in which an effect was always obtained from the lateral column of the same side, are due to the fact that the nerve investigated was left in connection with the cord by fibres emerging from at least three posterior roots, beside the 7th lumbar, but as we have not been able to carry the investigation of this point further at present, we would merely emphasize the fact that the anatomical connections with the cord were different in the two cases.

(3.) *Summary of the Facts in* (1) *and* (2).

If now we sum up the results of all these experiments when the nerve investigated is connected with the cord by afferent tracts only, we find that the average effect evoked by excitation of the posterior column of the same side

$$= \frac{147 + 156 + 108 + 28}{4} = \frac{439}{4} = 110,$$

the posterior column of the opposite side

$$= \frac{4 + 39 + 50 + 10}{4} = \frac{103}{4} = 26,$$

the lateral column of the same side

$$= \frac{10 + 20}{2} = \frac{30}{2} = 15,$$

the lateral column of the opposite side = 0.

That is to say, as far as these readings go, of the sum of all the effects obtained, the posterior column of the same side was concerned with 110/151 = 72 per cent. of the effect in the nerve;

The posterior column of the opposite side was concerned with 26/151 = 17 per cent. of such effect;

The lateral column of the same side with 15/151 = 10 per cent. of the effect;

The lateral column of the opposite side with no part of the effect.

It is most remarkable how nearly these average figures resemble those obtained by exactly similar average methods when the whole mixed nerve was the part investigated.

This similarity suggested to us the possibility that the fibres in the anterior roots are but slightly concerned in the production of the electrical effect in the mixed nerve when the cord is excited by such strengths of stimulus as have been used in the foregoing experiments (500–2000, very rarely 4000).

It will be found on referring to Chapter VI., that whereas the electrical effect observed in the cord to follow excitation of the cortex is very considerable, it is very small in the sciatic nerve, and we there suggest that this difference involves a change in the amount, intensity, or quality of the nerve impulses in their passage through the unknown endings of the pyramidal tracts, and the known origins of the efferent nerves, the anterior cornual corpuscles. (See fig. 22, p. 495, Chapter XI.)

To what extent, and under what circumstances, electrical effects can be detected in the sciatic nerve, when all the posterior roots are divided and the nerve is connected with the cord by efferent fibres only in the anterior roots, becomes therefore a most interesting question.

To the consideration of experiments upon this point we will now turn.

Section 5.—The Electrical Effects in Efferent Nerves following Excitation of the Spinal Cord.

The least complicated mode of experimentation for determining these effects would be that of directly observing the changes in the central end of a divided anterior root. This experiment, however, we have not yet successfully accomplished; the difficulties in the way of obtaining satisfactory connections with a divided anterior root are augmented by its anatomical relations, and by the fact that, in order, as we shall see, to obtain any changes in the root an intensity of stimulus has to be applied to the cord which evokes general movements, thus dragging on the short root. The dangers of inadequate isolation have been already dwelt upon in Chapter IV. Our attempts in this direction were so unsuccessful that we determined to employ the more laborious method of division of all the posterior roots, and examination of the electrical changes in the sciatic nerve.

The plan of experiment, therefore, consisted in exposing the lumbar cord and cauda equina (see Plates 34 and 35, and fig. 18), and then dividing the posterior roots of the 4th, 5th, 6th, 7th lumbar, 1st and 2nd sacral nerves, so as to leave the sciatic connected with the cord by the efferent fibres only.

We made experiments upon seven animals (Cats) on these lines; but in two of these we unfortunately did not divide the 5th lumbar posterior root and the connection

with the 4th, which, as the figure of the plexus shows, possibly furnish some, though a very small proportion, of the efferent fibres of the sciatic nerve.

The results of these two experiments are, therefore, not completely to the point, but they are interesting as showing the increase in the relative size of the effects obtained with excitation of the posterior column on the opposite side of the nerve, and of the lateral column on the same side, in comparison with those evoked from the posterior column of the same side.

The section of these posterior roots has thus cut down the preponderating effect obtained with excitation of the direct fibres in the posterior column.

Electrical Changes in the Sciatic Nerve after Section of the 6th and 7th Lumbar and 1st Sacral Posterior Roots on the Left Side.

	Intensity of stimulation.	Effect in nerve following excitation of			
		Posterior columns same side.	Posterior columns opposite side.	Lateral columns same side.	Lateral columns opposite side.
Cat (204) .	1000	58	70	40	0
		85	120	45	0
Cat (207) .	2000	30	5	2	0
	4000	110	43	12	0
		11	25		
		294	263	99	
	Average .	59	53	25	

The excitation of the anterior columns produced no effect.

The results are, however, probably mixed, as will be seen by reference to the experiment on the remaining animals.

In these all connections of the sciatic nerve with the cord, except the anterior roots, were divided; the interesting fact then came to light that, even with a strength of stimulus above that employed in the previous experiments, very small electrical effects were evoked in the nerve by cord excitation, these being evoked by stimulation of the posterior column of the same side and the lateral of the same side. When, however, the strength of stimulus was increased very markedly, effects were produced which were more marked in the case of the lateral. It is not, therefore, until the intensity of the stimulus is far beyond the limits hitherto used that any marked nerve effect is produced by the passage of impulses from the cord down efferent nerve fibres.

This is illustrated by the following experiment upon a Cat (209), the cord being cut at the 11th dorsal, and all the posterior roots on the right side divided as

described. With a stimulus of 2000, effects in the right sciatic nerve were observed only from excitation of the posterior and lateral columns of the same side, the deflections amounting to an average of 10 only. On increasing the stimulus to a considerable strength (4000) a deflection of 70 was produced by the excitation of the lateral column of the same side.

Still more striking experiments are the following made upon two animals (Cats), which may be set out in detail, the necessary strength of the stimulus employed being noteworthy.

EFFECT in Efferent Nerves following Excitation of Spinal Cord.

Animal.	Cord cut at	Strength of stimulus.	Excitation of posterior column of same side.	Excitation of posterior column of opposite side.	Excitation of lateral column of same side.	Excitation of lateral column of opposite side.
Cat (195)	13th dorsal vertebra	4000	0	0	6	0
		8000	10	17	50	2
			2		32	
Cat (191)	10th dorsal vertebra	4000	12	0	18	
			6	0	35	
		5000	14	0	40	
		6000	12		60	
			30		40	
	Fresh section	5000	15	0	36	
	11th dorsal	6000	28		35	
			11		45	
			9	6	56	0

In the preceding experiments with afferent fibres, the maximal intensity of the stimulus was that represented by .2000 ; the great increase in the intensity of the cord stimulus necessary to evoke effects in the nerve through efferent fibres is, therefore, very striking.

Another animal (Cat) which was experimented upon in the same way, must be considered as furnishing rather doubtful evidence, since we had previously not only exposed and excited the cut ends of the various divided posterior roots on the side of the nerve in order to obtain reflex effects, but had divided all the anterior roots on the opposite side of the cord. These operations must, from their severity and extent, have altered the excitability of the cord itself. As far as they go, however, the results are in accordance with those just set forth, since a stimulus of considerable intensity (3000) was necessary to evoke any effect in the nerve which, in the case of excitation of both posterior columns amounted to 30, and in that of the lateral column of the same side to 36.

Finally, in order to avoid the changes in excitability following immediate section of the posterior roots, those belonging to the 5th, 6th, 7th lumbar, and 1st sacral nerves, were divided on the left side in a Cat (227) 26 days before the experiment. When

examined at this later date, the animal was found to move in an ataxic manner, but was not paretic; the sensibility of the left hind limb was very much diminished, and the left knee jerk was absent.

The histological examination of the cord showed at the lesion on the left side degeneration of (*a*) fibres entering the posterior cornu, (*b*) fibres in the posterior cornu, (*c*) fibres in the posterior root zone, (*d*) fibres in the posterior external column. Higher up, at the 11th dorsal vertebra, there was no degeneration in the entering fibres, but a large cornu-shaped patch of degeneration in the left posterior external column. The left posterior median column showed no definite degeneration until the lower cervical region was reached.

The experimental results were obtained by dividing the cord at the level of the 10th dorsal vertebra, and preparing both sciatic nerves for connection with the galvanometer. Each nerve when excited evoked electrical changes in the observed region, the left one (on side of lesion) more than the right. On stimulating the columns of the cord, and observing the effect on the left nerve, it was found that, with the ordinary strength of stimulus, very slight effects of 4 and 8 followed excitation of the posterior column of the same side, and no effects were obtained with this strength of stimulus from either the lateral of the same side or the columns of the opposite side.

On the other hand, in the right nerve, effects of 35 and 56 were evoked by stimulation of the right posterior, and varied effects from 2 to 65 on stimulation of the right lateral.

The observation could not be repeated with stronger stimulus owing to the failure of the animal.

An examination of all these results and comparison with those of Sections 3 and 4, will show that the effects aroused in the mixed nerve by stimulation of the spinal cord must be mainly due to nerve impulses travelling from the cord down the afferent (sensory) fibres; since the effect due to impulses travelling down exclusively efferent (motor) fibres, in the first place, is very small in amount and, in the second place, is only produced by a strength of stimulus in excess of that employed in the experiments on the mixed nerve, and finally, is then mainly evoked by stimulation of the lateral tract of the same side as the nerve under observation.

Section 6.—The Influence upon the Electrical Effect in the Nerve of Intervening Sections in the Cord.

The experimental results to be studied under this heading throw more light upon the relations of the sciatic nerves to the spinal cord.

In the foregoing three groups of experiments, whilst excitatory electrical effects were evoked in the afferent, efferent, and mixed nerves by stimulation of the different columns in the cord, no direct evidence was afforded of the nature of the path in the cord along which the impulses, starting from the excited cross section

of any one particular column, pass to reach the nerve roots. It cannot be assumed that the result of the excitation of any particular column is to evoke nerve impulses which, in their passage to the issuing nerve roots, are limited to fibres in this particular column, or that any particular excitation, however strictly localised, may not excite by commissural fibres a neighbouring column. Indeed, as far as the cord itself is concerned, the evidence afforded by the experiments (Chapter VIII.) shows there is no absolute limitation of descending impulses to one column.

It is, therefore, a matter of great importance in connection with the present investigation to ascertain to what extent in the foregoing experiments the path of such impulses as issue by the nerve roots is limited in the cord to the particular column stimulated. We endeavoured to obtain information as to this in the following manner: we first made experiments with the mixed nerve precisely similar to those already described (Section 3), that is, we connected the nerve with the galvanometer circuit, and excited the cut ends of the various columns of the cord, as displayed in a transverse section. We then made a section of one column between the seat of excitation and the lumbar roots of the sciatic nerve, and repeated the first experiment under these conditions. We were thus enabled to ascertain how far the nerve effect due to the excitation of any particular column was reduced when the fibres of that column were all cut through. Any remaining effect might be due to—

(*a.*) The presence of fibres which passed from the stimulated into other columns;

(*b.*) The presence of fibres connected with the corpuscular portion of the cord, and the awakening of the same by their means, the nervous impulses thus reflexly discharged proceeding either along fibres in other columns or along fibres in the same column below the interruption.

To what extent these various factors come into play will be made evident by a careful analysis of all the results. These are best grouped in accordance with the particular part of the cord which was the seat of the intervening section.

A. *Influence on the Effect in the Nerve of Hemisection of the Cord.*

The first group of results show that an intervening hemisection of the cord completely abolishes the nerve effect produced by excitation of the columns on the side of section, as well as that evoked by excitation of the posterior column of the opposite side.

Thus the spinal cord was exposed and divided in a Cat (329) at the level of the 9th dorsal vertebra; both sciatic nerves were now prepared for galvanometric observation, and the electrical effects obtained by exciting the cut section of the various columns at the 9th dorsal vertebra observed, the results being given as under.

Nerve observed.	Column of cord excited.			
	Excitation of left posterior.	Excitation of left lateral.	Excitation of right posterior.	Excitation of right lateral.
Left sciatic nerve observed, diff. = ·012 Daniell . .	Deflection 85	10	25	0
Right sciatic nerve observed, diff. = ·011 Daniell . .	„ 22	0	89	9
Hemisection of cord on left side at level of 1st lumbar vertebra.				
Left nerve observed . . .	Deflection 0	0	0	0
Right sciatic nerve observed	„ 5	0	130	8

The above experiment thus shows that with such an intensity of stimulus as that used (1000) the result of an intervening hemisection on the same side as the nerve is to abolish the nerve effect. If it is on the opposite side of the nerve, then the only effect interfered with is that evoked by the stimulation of the posterior column on the side of the lesion. It would therefore appear that with this strength of stimulus the nerve impulses, which subsequently cause the electrical effects, are localised to one side of the cord in both the area of stimulation and the subsequent path through the cord from that area to the issuing nerves.

There is, however, one point to which it is desirable to draw attention before proceeding to the next experiments. This is the absence of any effect in the left nerve when, with a hemisection limited to the left side, the right posterior column is stimulated. We do not interpret this as implying that there is no crossed path from the opposite posterior column to the roots of the lumbar nerves, but that either such crossing has to a great extent occurred at a higher level than the 1st lumbar vertebra, the level of the section, or that the hemisection had either directly (by injury) or indirectly lowered the excitability of the neighbouring posterior column, and that thus the intensity of stimulus used was inadequate to evoke nerve impulses which could pass down the afferent fibres of such an indirect path as connects this column with the nerves on the opposite side. This latter supposition is rendered not improbable by an experiment made upon an animal (Cat, 283)* in which the hemisection had been performed four months before the experiment. The cord of this animal was exposed and divided for excitation at the 10th dorsal (the hemisection had been made on the left side at the 12th dorsal). The electrical effects produced in the two nerves by excitation of the different columns (coil 2000) were as follows :—

* For full description of this animal during life and after death see pp. 429–430.

	Exeitation of left posterior.	Left lateral.	Right posterior.	Right lateral.
Cat (283).				
Left nerve	0	0	35	0
Right nerve	0	0	82	15

In this case the previous hemisection had rendered excitation of the columns on the side of the lesion quite ineffectual, as far as the generation and propagation of nerve impulses into either nerve were concerned. The excitation of the posterior column on the opposite side to the lesion, however, evoked effects in both nerves. It would, therefore, appear that the crossing through grey matter from the one posterior column to the other, and so to the nerves, was in this case below the level of the hemisection, viz., 12th dorsal vertebra. This experiment apparently is contradictory in its results, as regards the crossing from the opposite posterior column, to that just given; but putting aside the presence and absence of immediate shock in the two cases respectively, it must be remembered that the lesion in this case was two vertebræ higher up. The localisation to the particular column excited of the generated impulses at the area of stimulation is very clearly brought out by this experiment, as well as the failure of production of any crossed effect from the sound (right) lateral column into the left nerve.

B. *Influence on the Nerve Effect of Section of the Posterior Column on the Same Side as the Nerve Observed.*

The influence of the section of one of the posterior columns will be here considered before that due to section of both, for although its effects are more complicated, the experimental procedure by which the changes were produced involved the section first of one and then of the other column. It will be found that the result is extremely definite as regards the particular column operated upon, as the following experiments upon two animals, Cat and Monkey, show. It will be noticed that a considerable intensity of stimulus was necessary to produce effects in the Monkey.

SECTION of one Posterior Column on the same side as the Nerve. Left Sciatic Nerve observed.

	Column of cord excited.			
	Excitation of left posterior.	Excitation of left lateral.	Excitation of right posterior.	Excitation of right lateral.
Cat (311)				
Cord divided at 9th dorsal vertebra				
Stimulus 500.	130	0	20	0
	132	0	26	0
Left posterior column cut at 1st lumbar vertebra	0	0	10	0
Stimulus 500.	0	0	5	0
Monkey (333)				
10th dorsal	106	25	39	2
Left posterior column cut at 12th dorsal vertebra				
Stimulus 4000	3	18	12	2
	6	20	10	0

In these two cases an intervening section of the posterior column on the side of the nerve observed had the effect of entirely abolishing, or diminishing to a mere trace, the large nerve electrical change which was formerly produced by the excitation of that column It may therefore be inferred, that the fibres which connect the posterior column at the level of the 10th dorsal vertebra with the posterior roots of the lumbar nerves on the same side, run wholly in that column, and that the stimulation and the path are strictly localised therein.

There is, however, a further result, that, namely, shown by a diminution in the nerve change evoked by stimulation of other columns. This may be due either to the cutting off of crossing fibres, or to a depressed condition in the excitability of the remaining part of the cord.

It is improbable, however, that both the latter causes operated in these cases, since when we group together in the next table the influence of the lesion upon the electrical changes in the nerve of the opposite side, although we obtain in both animals evidence of diminution, yet the condition of the Monkey after the section was evidently one of more and not less excitability than it was before, since the uninjured right posterior column evoked larger effects than it did in the normal state. (See Hyperexcitability after Section, Chapter IX., Section 7, C.)

C. *Influence of Section of the Posterior Column on the opposite side to the Nerve observed.*

RIGHT Nerve observed.

	Column of cord excited.			
	Excitation of left posterior.	Excitation of left lateral.	Excitation of right posterior.	Excitation of right lateral.
Cat (311)				
Cord divided at 9th dorsal vertebra	36	0	108	0
Left posterior column cut at 1st lumbar vertebra	4 2	0	48 37	0
Monkey (333)				
Cord divided at 10th . . .	52	4	112	15
Left posterior column divided at 12th dorsal vertebra	30	0	150	15

It is seen that the effect evoked in the nerve by stimulation of the posterior column of the opposite side is diminished by section. The diminution cannot be attributed to general lowering of excitability since it is present in both cases, and it will be seen that in the Monkey the excitability of other columns had increased. It must be due to the interruption by the lesion of fibres crossing through indirect channels from that posterior column. As this interruption occurs in the posterior column, it would imply that there are fibres which cross over from one posterior column to the other, which have a wide distribution along the cord. The diminution is due to the cutting off of such fibres as descend to cross below the level of the respective sections; the effect still obtained after the section may be due to those fibres which, having crossed above the level of the same, are not interrupted by the lesion. Reference to the spinal cord experiments (Chapter VIII.) will show that according to our experiments the fibres in the two posterior columns have very extensive indirect connections with each other.

D. *Influence of Section of both Posterior Columns on the Electrical Effects evoked in the Nerve.*

When both posterior columns were divided, mere traces of nerve effect were evoked by excitation of either column, even when the stimulus was sufficiently intense to produce marked effects from stimulation of the lateral column on the same side as the nerve.

This is shown by the following experiments made upon the same two animals, the nerve effect due to excitation of each different column being compared before and after the intervening section of the posteriors.

Nerve observed.	Column of cord excited.			
	Excitation of left posterior.	Excitation of left lateral.	Excitation of right posterior.	Excitation of right lateral.
Cat (311)				
Section of 9th dorsal		Before	26	0
Left nerve (stimulus 500) .	152	0	20	
	130		81	8
Right nerve.	16	0		
Section of both posteriors at 1st lumbar		After	0	
Left nerve (stimulus 1000)	0	30	18	5
Right nerve.	0	0	0	0
Left nerve (stimulus 2000)	0	65		
Monkey (333)				
Section at 10th dorsal		Before	112	6
Right nerve (stimulus 4000)	52	4		
Section of both posteriors at 12th dorsal		After	6	21
Right nerve (stimulus 4000)	6	0		
Cat (251)*				
Section, 1 month previous, at 10th dorsal				
Right nerve (stimulus 4000)	0	10	0	35

It is evident that the interruption, as far as the posterior column is concerned, is now practically complete for both nerves, hence all the fibres by which these columns are connected with the lumbar nerve roots are now severed, and thus any crossing of nerve impulses out of either posterior column into the lateral columns, or into any structure except the other posterior at a level higher than that of the 12th dorsal, is negatived.

It remains now to see the influence of section of the lateral column upon the effect.

E. *Influence of Section of the Lateral Columns on the Electrical Effects evoked in the Nerve.*

The limitation of the area of stimulation, and the localisation of the descending nerve impulses to the fibres of the excited column, are apparently very complete in the case of the lateral column, so far as the records of muscular movements can show. (*Cf.* SCHIFF, see p. 347.)

It remains to be seen to what extent this is true of the particular impulses now studied which, as our previous remarks have shown, must be considered as conveyed into the nerve by the posterior as well as the anterior root fibres.

* For full description of this animal, *i.e.*, appearances during life and death, see *b*. 439.

The experiments upon this point were made upon two Cats, in one of which (259)* the lateral column had been divided 34 days previous to the experiment, whilst in the other an intervening section was made of all structures except one lateral column at the time of the experiment.

The results of the experiment in the first case are given in the adjoining table:—

LEFT Lateral Column divided 34 days before Experiment, at 10th Dorsal Vertebra.

Nerve observed.	Column of cord excited.			
	Excitation of left posterior.	Excitation of left lateral.	Excitation of right posterior.	Excitation of right lateral.
Cat (259).				
Section at 4th dorsal vertebra				
Left sciatic observed—				
Stimulus 1000	35	0	0	0
	48	0	12	0
2000	22	0	52	0
Right sciatic observed—				
Stimulus 1000	20	0	40	0
2000	42	0	78	28

It will be noticed that no change at all in the left nerve followed excitation of the left lateral column, although, in the right nerve, a change was evoked from the right lateral column. Since, however, nerve effects are not easily evoked from the lateral column by moderate stimuli, and when these are employed strong violent reflex effects are produced by stimulating other columns, it was desirable to adopt a different procedure and make an intervening section of such character as would divide all fibres except those in one lateral column, which could then be used as a standard of comparison.

The results before and after such division are shown in the following table:—

* For full description of this animal as regards its appearances during life and after death, see p. 405.

Nerve observed.	Column of cord excited.			
	Excitation of left posterior.	Excitation of left lateral.	Excitation of right posterior.	Excitation of right lateral.
Cat (363)				
Section at the 9th dorsal vertebra.				
Left nerve.				
Stimulus 500	42	0	8	0
1000	122	0	10	0
2000	138	0	28	0
Section of all columns except right lateral at 12th dorsal.				
Stimulus 2000	0	0	0	0
4000	0	0	0	14
Right nerve. Before section.				
Stimulus 500	5	0	95	0
2000	28	0	145	0
Section of all columns except right lateral at 12th dorsal.				
Stimulus 2000	0	0	0	0
4000	0	0	0	28

In these experiments, it is seen that the right lateral column was excluded from the section, and that stimulation of no other column above the section, except the right lateral, produced any nerve effect.

It has, however, been shown in Chapter IX. that when impulses proceed up the posterior roots into the cord they are conveyed to some extent (20 per cent.) by the lateral columns of the same side. A connection between the posterior root fibres and the lateral column, presumably by means of fibres in the posterior column or cornu, must therefore exist. This connection is, however, of such a special kind that it offers an evident resistance to the passage of impulses backwards from the cord into the root. The fact that no effects in the above experiment could be obtained when, with the lateral column as the sole bridge between the excited upper portion of the cord and the nerves, the posterior columns were excited, shows that any spread of path from the posterior to the lateral columns, if it exists, must either be below the level of the section (12th dorsal) or must offer a resistance to the passage of impulses in the downward direction which it does not offer to their passage in the upward direction, that is, in their ascent towards higher centres.

The relations which the cord columns appear to have with one another, as given in the summary of Chapter VIII., are in this respect of great interest and importance.

Two results are clearly brought out by the consideration of the series of experiments in the whole of this section; the first that the analogous character of the general electrical results in cord and nerve, without being pushed too far, may be extended to this point, that the stimulation of any one column in the cord is a localised stimulation of the nerve fibres in that column only, and the second, that the resulting nerve

impulses generated at the seat of stimulus are propagated to the root of the nerves along fibres constituting direct and indirect tracts, which are for the most part confined to the particular column which has been excited; the sole exception being that of the posterior column on the opposite side to that from which the nerve roots spring.

Section 7.—Summary and Conclusions.

The experimental results detailed in this chapter form a sequel to those of the preceding Chapter IX., as to the relations which exist between the lumbar nerves and the spinal cord. Complete harmony between the results of the two series of experiments is not to be expected from the very different physiological and anatomical conditions which they involve. It will, however, be seen, if we compare the present results with those given in the summary of Chapter IX., that as regards the main points the one set form a corollary to the other.

In order that the salient features of the two should be clearly expressed, the following Table, in which all the results of the present chapter are massed under different heads, is laid before the reader.

The Table shows the average percentage of the total amount of the effect which has been observed in the sciatic nerve, or its roots, when each lateral and posterior column of the cut cord is respectively stimulated.

The same average percentage is also shown, when the stimulus is minimal, in a separate appended table.

I.—The Amount per cent. of the Total Nerve Effect evoked by adequate Cord Stimulation due to Localised Excitation of Particular Columns.

Character of nerve connected with galvanometer circuit.	1. Excitation of posterior column of same side.	2. Excitation of lateral column of same side.	3. Excitation of posterior column of opposite side.	4. Excitation of lateral column of opposite side.
	Per cent.	Per cent.	Per cent.	Per cent.
Posterior root	85	3	12	0
Mixed nerve sciatic . .	73	9	15	3
Sciatic Nerve with anterior roots cut . . .	73	10	17	0
Average	77	7	15	1

II.—The same when the Cord Stimulation is Minimal.

Character of nerve connected with galvanometer circuit.	1. Excitation of posterior column of same side.	2. Excitation of lateral column of same side.	3. Excitation of posterior column of opposite side.	4. Excitation of lateral column of opposite side.
	Per cent.	Per cent.	Per cent.	Per cent.
Posterior root	97	0	3	0
Mixed nerve.	84	0	16	0

If these results are to be relied upon as indicating not merely different amounts of electrical change, but the presence of different amounts of nerve impulses propagated from the stimulated area along the cord and into the observed nerve, then their main features indicate the following relations between the dorsal cord and the sciatic nerve in the case of *cord-to-nerve* experiments:—

(1.) The path of least resistance, as shown by "minimal" stimulation, between the cord and the afferent fibres of the sciatic nerve, is that of the posterior column of the same side; this path being that of the directly continuous afferent fibres.

(2.) Of the indirect nerve paths between the cord and the afferent fibres, the path of least resistance is that of the posterior column of the opposite side, as is shown also by Table II.

(3.) The afferent paths, direct and indirect, along which nerve impulses can be made to travel (*backward*) from the stimulated cord to the sciatic nerve, have the following relations to the posterior roots of the sciatic nerve, as shown in Table I:—

(*a.*) The posterior column of the same side conveys 77 per cent. of the amount of nerve impulses;

(*b.*) The lateral column of the same side conveys 7 per cent.;

(*c.*) The posterior column of the opposite side conveys 15 per cent.;

(*d.*) The lateral column of the opposite side conveys a mere trace.

We will now compare these deductions with those of the preceding chapter from *nerve-to-cord* experiments. These latter were briefly as follows:—

(1.) The spinal path by which afferent impulses proceeding up the nerve travel in the cord is, when these impulses are generated by "minimal" excitation, almost entirely that of the posterior column of the same side, *i.e.*, the directly continuous one.

(2.) Of the indirect spinal paths along which such ascending impulses travel, that in the lateral column is the path of least resistance of the same side.

(3.) All the afferent spinal paths have the following relations to the posterior roots of the sciatic nerves as regards the transmission of afferent impulses generated in the fibres of the sciatic nerve:—

(*a.*) The posterior column of the same side conveys an average of 60 per cent. of the total amount (intensity and quantity) of nerve impulses;

(*b.*) The lateral column of the same side conveys 20 per cent.;

(*c.*) The posterior column of the opposite side conveys 15 per cent.;

(*d.*) The lateral column of the opposite side conveys 5 per cent.

The following features of these two sets of deductions are similar:—

i. That the channel of connection with the posterior roots is *par excellence* that of the fibres in the posterior column of the same side;

ii. That what crossing does exist is almost entirely due to indirect continuity with the fibres in the posterior column of the opposite side;

iii. That the crossed path represents only about 15 per cent. of the available path;

iv. That the fibres in the lateral column have very much closer indirect relations

with the fibres of the posterior roots on the same side than they have with those on the opposite side, these last being scarcely represented.

The most striking differences between all the connections of the posterior roots with the cord, as dependent upon whether impulses are made to ascend or descend them, are—

i. For ascending impulses the lateral column of the same side affords indirect channels of *greater* efficiency than the crossed path in the opposite posterior column, or, *a fortiori*, the opposite lateral column.

ii. For impulses descending along afferent paths the lateral column affords indirect channels of *less* efficiency than the crossed path in the opposite posterior column.

iii. The ease with which the ascending impulses evoked by "*minimal*" excitation cross from the posterior root into the posterior column of the opposite side is considerable as compared with that which characterises the passage backwards from a posterior column into the opposite nerve roots when descending impulses are evoked by such "*minimal*" excitation.

These differences tend to show that although there is no absolute block to the backward passage of impulses descending afferent channels into afferent fibres of the nerve, such as exists in the anterior roots to the passage upwards of ascending impulses in efferent channels, yet there is a physiological difference between the facilities which afferent indirect paths offer to the passage of impulses, this passage being much easier when it occurs in the normal ascending direction.

We now consider ourselves warranted in concluding that, as far as the afferent tracts are concerned, the deductions of Woroschiloff, Miescher, &c., referred to on p. 420, are founded on experimental results which, from their nature, readily admitted of misinterpretation, and that both physiological experiment and anatomical investigation point with great distinctness to what is the true afferent path. Our observations confirm the views as to the physiological properties of the posterior columns set forth in 1847 by Longet and reasserted by Schiff, with this modification, that although the posterior columns form the main path of connection between higher portions of the cord and the posterior roots of the nerves, yet there is a path in the lateral column which is strictly confined to the side of the entering roots.

It may be urged that there are pathological cases (Brown-Séquard) which undoubtedly exist, of motor paralysis on one side and hemianæsthesia on the other, following a local lesion of the cord. In reply, we can only state that we believe much more definite evidence than that afforded by the existing clinical data must be forthcoming in order to shake the solidity of the foundations for our propositions, a solidity derived from the welding together of all the foregoing quantitative results of exact experiments. We therefore are compelled to regard the above clinical experiences as either in no way indicative of the normal relations of the cord to the nerves, or as capable of explanation on the supposition that the lesion has affected at the same time

the motor path (lateral column) on one side and the principal afferent path (posterior column) of the opposite side.

Finally, the results of the foregoing sections have brought to light some interesting details as regards the relation of the cord to the efferent nerves.

In the Table it will be noticed that the results, obtained with "minimal" stimuli, as regards the sciatic nerve, are not affected by section of its anterior roots; hence, as far as the cord stimulation in these experiments extended, no nerve impulses passed down the motor roots capable of causing perceptible electrical changes in the nerve except with strong stimuli.

As far, then, as the localisation of the path of efferent fibres in the cord is concerned, the present investigation has at present gained no further information; the lateral column on the same side as the issuing nerve is the main path for outgoing nerve impulses in the lumbar nerves. But the method has brought to light a remarkable characteristic of this path, namely, that at one portion, that which connects in the spinal nerve-centres the pyramidal nerve fibres with the origins of the anterior root-fibres, it exercises such a modifying influence upon the traversing impulses that these issue so altered in number, intensity, or quality, as to cause but very slight electrical effects in the nerves, and that it is not until a comparatively strong stimulus is used that the issuing impulses are of such kind as to cause really appreciable nerve effects.

This brings us to the subject of the next chapter, which deals with the physiological relations between the nerve-corpuscles and the nerve-fibres.

CHAPTER XI.—ON THE FUNCTIONAL ACTIVITY OF NERVE CENTRES AS EVIDENCED BY THE PRESENT METHOD.

Section 1.—The present state of knowledge of the relations of the nerve centres in the cord.
(1). Anatomical. (2). Physiological.
Section 2.—Experiments by the galvanometric method directly bearing on the spinal nerve centres.
1. Resistance offered by the efferent side of the centre to the passage of impulses.
2. Resistance offered by the afferent side to the passage of impulses.
Section 3.—Character of the impulses discharged by the spinal centres.
Section 4.—The influence exerted upon the electrical changes in a directly-excited nerve by its attachment to the spinal cord.
Section 5.—The spread of reflex discharges up and down the cord (internuncial fibres).
Section 6.—On the electrical changes in the cortical nerve centres.
Section 7.—Summary.

Section 1.—The Present State of Knowledge as to the Relations of the Nerve Centres in the Spinal Cord.

The employment of the galvanometric method to estimate quantitatively the

excitatory state of the nerve channels or fibres in the cord led us to attempt to apply it as a gauge of the conditions prevailing in and between the spinal centres.

Even a careful review of the history of the subject fails to show absolutely more than a few facts from which knowledge of the actually intracentral processes may be drawn. We will now present in a brief sketch what is understood from anatomical and physiological evidence to fairly represent the structure and functional activity of simple nerve centres, such as those in the spinal cord, in order that the bearing of our own observations may be more comprehensible.

1. *Anatomical Relations.*

The most recent anatomical investigations by GOLGI, HELD, FLECHSIG, and others, chiefly by means of the methods of staining devised by GOLGI, have established the justification for regarding a nerve centre in the spinal cord as constructed as follows :—

(*a.*) An afferent side ("sensory"), to which run afferent channels from the posterior root.
(*b.*) Field of conjunction between the afferent and efferent sides.
(*c.*) An efferent side consisting of large nerve corpuscles, from which issue the efferent channels.

(*a.*) Examined in further detail it appears that, of the afferent channels running into the spinal cord from the posterior roots, some ascend directly in the posterior and postero-median columns, others enter the posterior cornu of grey matter, and are lost therein, others pass through the grey matter far into the anterior cornu of the same.

Further, the afferent side is composed of a ground basis, fibres, and corpuscles, the branches of which cannot be traced soon after their subdivision.

(*b.*) The field or area in which connection exists between the two sides of a nerve centre is differently accounted for by various observers. All, however, are agreed that the central branches of the large efferent so-called motor corpuscles repeatedly subdivide towards the afferent side, and tend to form what was formerly described as a network (GERLACH), but the anastomosis of the elements of which appears to be more and more doubtful with further knowledge. (The actual mode of conjunction between the afferent side and these branches of the efferent corpuscles is, therefore, unknown ; but it is easily conceivable that as much as is known, *i.e.*, subdivision, &c., may very properly be regarded as the seat of higher resistance, and we believe that this field of conjunction is the region in which should be localised what we subsequently express as the "block" to the passage of functional impulses.)

(*c.*) The elements on the efferent side have been long known as the "motor" part of the nerve centres. The large corpuscles, recognised by many authors to be distinctly

fibrillated in their intimate structure,* shew a peculiar arrangement of one medullated outgoing branch, and from the opposite side numerous subdividing branches.

Spinal Ganglia.—A word must here be interpolated on the structure of the ganglion of the posterior root in its character as a simple nerve centre.

All research† on the anatomical structure of these ganglia goes to show that their corpuscles pass through a change in the course of their development, being at first bipolar and afterward unipolar, and that any axis cylinder in relation to any such corpuscle does not directly enter this but gives off a branch at right angles to the ganglion cell, thus forming what has been termed a T-shaped junction.

In addition, it has been shown‡ that there are fibres (as "determined" by the degeneration method) which pass through the ganglion (spinal) into the posterior root without coming into any relation with its cells. To sum up shortly, therefore, it is evident that there are passing through a spinal ganglion numerous direct protoplasmic nerve channels.

We have now to sketch further the afferent and efferent relations of the spinal nerve centres with the encephalon, with the other centres in the spinal cord, and with the periphery.

Afferent Channels of Communication.—The afferent paths may advantageously be considered in reverse order to that just given.

The afferent fibres in the posterior root are now known to have the following destinations as regards the spinal nerve centres:—

1. Some pass the centres and, without communicating with them, enter the postero-external column and finally course up the postero-median column to the nucleus gracilis.
2. Others enter CLARKE'S column where that is present.
3. Others enter the posterior horn, and are lost in it.
4. Others enter the posterior horn, but pass through it to enter the anterior horn.
5. Some fibres bifurcate on their entry into the cord, one branch ascending and one descending; the branches end in a fine plexus in the grey matter (KÖLLIKER).

The different fibres leaving the spinal nerve centre to connect with its neighbour have never received absolute anatomical demonstration, but from the results of physiological investigation their existence must be postulated.

The afferent fibres connecting the spinal nerve centres with the encephalon have been determined by the degeneration method to pass up the direct cerebellar and antero-lateral tracts and have been traced as far as the cerebellum and pons, but no further.

* See particularly MAX SCHULTZE, and H. SCHULTZE, 'Archiv f. Anat. u. Physiol.' FLEMMING. HENLE'S 'Festschrift.'

† See particularly RANVIER, 'Traité Technique d'Histologie.' HIS, 'Tageblatt der Naturforscher Versammlung zu Berlin, 1886.' FRITSCH, 'Archiv f. Mikrosk. Anat.,' vol. 27, 1886.

‡ MAX JOSEPH, 'Archiv f. Anat. u. Physiol.' (DU BOIS-REYMOND), 1887, p. 307.

Efferent Channels of Communication.—The efferent path from the encephalon, *i.e.*, cerebrum, is well known as the pyramidal tract, and the fibres composing it are commonly supposed to end in the corpuscles of the anterior horns. As this connection is of the utmost importance, we may be permitted to discuss the point at a little further length.

The evidence by the degeneration method shows that the principal mass of the pyramidal tract fibres do not run towards the corpuscular elements in the anterior or ventral horn, but towards the *posterior* or dorsal portion of the nerve centres, thus suggesting that the fibres join rather the field of conjunction than the efferent side. Again, the degeneration method shows clearly that no pyramidal fibres pass directly out into the anterior root.

Anatomically therefore there is evidence of some structural change in the path where the pyramidal fibre comes into relation with the spinal centres.

The distribution of the pyramidal fibres in the spinal cord is still so much a matter *sub judice*, especially after recent work by the histological* methods, that the complete destination of the fibres, when yet at the upper part of the cord, is unknown.

The existence of efferent fibres (internuncial) connecting each nerve centre with the next and others below it have, like the afferent internuncial system, been surmised to exist from physiological evidence, all anatomical facts being wanting.

We believe that our previous experiments (see bilaterality, &c.) go to show that such efferent internuncial fibres must be few in number and but feebly differentiated.

The efferent channels from the spinal nerve centres are the fibres composing the anterior roots.

Commissural Channels of Communication.—Of commissural connection between spinal nerve centres of opposite sides of the cord no certain anatomical proof exists, but the presence of such connection is surmised from the physiological evidence, and is morphologically suggested by many researches, especially those of Lockhart Clarke and Golgi.

2. *Physiology.*

While the spinal nerve centres have been investigated in numerous ways since Wundt† estimated the delay in the passage of an impulse through them, it is remarkable how little is known with certainty of their functional activity.

By the galvanometric method we have been able to establish some fundamental considerations on this matter, and, to indicate their bearing, we will first enumerate categorically the facts that have been previously ascertained by various investigators.

The facts may be conveniently divided under the headings of—

* See particularly C. Golgi, 'Anatomischer Anzeiger,' 1890, Nos. 13 and 14, and C. Sherrington, 'Journal of Physiology,' &c.

† Wundt, 'Untersuchungen zur Mechanik der Nerven und Nervencentren,' 1876.

A. Spinal ganglion.
B. Jugular ganglion of vagus.
C. Spinal cord nerve centres.
D. Channels of communication.

A. Owing to the fact that the spinal ganglion has been made the object of some important experimental observations we think it better to state these first, although they are not, in our opinion, to be placed on the same ground as the phenomena relating to the spinal nerve centres.

This latter position is justified on consideration of the anatomical structure of a spinal ganglion previously given, which shows that it is traversed by "through" protoplasmic channels.

(*a.*) *Transmission of the Excitatory Electrical Change.*

Du Bois-Reymond observed* that when excitation was applied on the proximal side of a spinal ganglion the "negative variation" was observable in the nerve trunk on the distal side.

(*b.*) *Delay in the Transmission of a Nerve Impulse through a Spinal Ganglion.*

Exner† considered that his observations on a spinal ganglion in the Frog, warranted the opinion that the delay in the transmission of the excitatory condition (negative variation) through a ganglion was the same as would be produced by its passage along a nerve fibre; that, in short, there was no special delay. As these observations were made with Bernstein's differential Rheotome, we agree with Gad that they may be possibly conditioned by summation.

(*c.*) *Trophism.*

As is well known since Waller's‡ classical experiments, the ganglion exercises a trophic influence on the afferent nerve channels§ running in the posterior root.

B. Before passing to the observations on the spinal cord nerve centres, we must specially allude to the valuable work by Gad and Joseph‖ on the subject of *delay* in a ganglion. The ganglion they chose was not a spinal ganglion, but its homologue, the jugular ganglion of the vagus in the Rabbit. By recording the instant of change in the respiratory movements when the vagus was excited, respectively on the proximal and

* 'Untersuchungen über thierische Elektricität,' 1849, vol. 2, 5, 601.
† 'Archiv für Anatomie und Physiologie.—Phys. Abth.,' 1877, p. 567.
‡ 'Comptes Rendus de l'Académie des Sciences,' 1851, &c.
§ Excepting the fibres described by Max Joseph.
‖ 'Archiv für Anatomie u. Physiologie,' Du Bois-Reymond, 1888.

distal sides of the ganglion, they established reason for believing that the impulses which affected respiration were delayed in transmission through the ganglion to the extent of ·036 second. As GAD and JOSEPH point out, these experiments are open to the criticism that the summation of subminimal stimuli may be an important factor in producing the result.

C. The conditions under which the functional activity of the nerve centres of the spinal cord, as indicated by muscular contraction, is evoked necessarily form the major part of the facts at our disposal.

These conditions may be arranged as follows :—

(1.) *Adjuvants.*—Warmth. Preliminary influence of cold. After effects of section of spinal cord* a little distance above the nerve centre. Some drugs, *e.g.*, strychnia, &c.

(2.) *Depressants.*—Prolonged fall of temperature. Shock after division of the spinal cord (greater in proportion to proximity of section to nerve centre).† Anæmia. Narcotic drugs (anæsthetics, &c.).

(3.) *Delay.*—A series of measurements have been taken of the time lost during the passage of a nerve impulse from one posterior root through a spinal nerve centre to the corresponding motor nerve of the same side. This delay, or time-loss, has been estimated by the majority of observers‡ to be about ·01 in the Frog. (EXNER, in man, bulbar reflex ·04 second). This refers only to the "direct reflex," *i.e.*, of the same side as the excitation.

The delay with the "crossed reflex" (see later paragraphs) is ·004 second longer than the direct.

(4.) *Mode of Discharge.*—A spinal cord nerve centre can be excited by a single induction shock if it be applied to an afferent channel. The effect produced as recorded by the contraction of a muscle is apparently that of a single twitch. If an interrupted current be applied to the spinal cord or an afferent channel, the effect similarly recorded is a continuous contraction.

An effect in the muscles of an intermediate form has been frequently recorded, viz., a rhythm, the rate of which has been determined to be, on the average, eight to ten per second.

Occasionally an after effect has been noted, *i.e.*, a few muscular responses after the spinal excitation has ceased, and in some cases these are continuous.

(5.) *Trophism.*—It is well known that lesions of the spinal nerve centres which involve the efferent nerves are attended by wasting and other evidences of failure of nutrition in the parts which are in relation with the centre in question.

* See FRANÇOIS FRANCK, *loc. cit.*; v. BEZOLD, *loc. cit.*, &c., &c.

† DE BOECK, 'Archiv für d. ges. Physiologie' (confirmed also by our observations).

‡ Particularly HELMHOLTZ, WUNDT, FRANCK, CYON, and others. *Loc. cit.*

(6.) *Summation of Stimuli.*—A most characteristic feature of the functional activity of a nerve centre is its property of summating (STIRLING) subminimal stimuli with the effect of producing an apparently complete discharge.

D. The channel of communication between a spinal and other centres may be briefly alluded to as follows :—

(*a.*) *Relation of one spinal nerve centre to another.*—It is not possible on this point to improve upon the classical "Gesetze" of PFLÜGER,* viz., that—

(1.) In a simple reflex the muscular response is always on the same side as the excitation.

(2.) If a reflex is bilateral, the analogous muscles of the opposite side are thrown into action.

(3.) If a reflex is bilateral, the movements on the side opposite to that stimulated are much weaker than those on the same side. (*Cf.* our results on p. 494.)

(4.) If associated reflex centres are excited, the association is found to have an ascending arrangement in the spinal cord, culminating in the medulla oblongata; whereas of the encephalic reflexes the association is of a descending character, and also culminating in the bulb.

(*b.*) *Conduction.*—SCHIFF† showed, by section of the crossed pyramidal tract, that the fibres running in it to the lowest spinal centres were undoubtedly the channels of conduction from the encephalon.

EXNER‡ came to the conclusion, by time measurements, that there was a delay experienced by the excitatory condition or impulse traversing the spinal centres, when, the descending tracts in the cord having been excited, muscular contractions followed; but he admits that his results do not permit of a demonstration of the amount of time lost.

SECTION 2.—EXPERIMENTS BY THE GALVANOMETRIC METHOD DIRECTLY BEARING UPON THE STRUCTURE OF NERVE CENTRES.

(1.) *Resistance offered by the Efferent Side of the Centre to the Passage of Impulses.*

The results which have been obtained by our method are best arranged according to the particular part of a nerve centre to which they appear to refer.

In considering the anatomical structure of a nerve centre as we have given it on p. 479, it is evident that the region of greatest obscurity is that which we have termed the area or field of conjunction between the afferent and efferent sides, and

* 'Die sensorischen Functionen des Rückenmarks der Wirbelthiere,' v. E. PFLÜGER. Berlin. 1853.

† 'PFLÜGER, Archiv,' vol. 30, 1883, p. 248.

‡ 'PFLÜGER, Archiv,' vol. 8, 1874, p. 537.

in which there is from physiological evidence reason to believe considerable delay occurs in the passage of the impulses through the centre.

Such histological evidence as has been referred to in Section 1 suggests that the structure is of such nature as not to facilitate the passage of impulses through this region, but when we performed the following series of experiments we were surprised to find the degree to which such hypothetical obstruction really prevailed. It occurred to us that the obstruction might be more marked to excitatory impulses passing in the *reverse* direction, *i.e.*, from efferent to afferent mechanisms. We were not at all prepared, however, to discover, as we have done, that that obstruction was actually an absolute block; nevertheless, such appears to be the case.

To ascertain this we arranged the experiment as follows :—

Having divided the cord at the level of the 10th dorsal vertebra (see fig. 19), we raised its peripheral end for observation as described in previous pages and connected it with the galvanometer by its cross section and surface. The cauda equina having been exposed to an adequate degree, a pair of nerve roots was selected (usually the 7th lumbar), divided just above the intervertebral foramen and their central end raised in the air by ligatures and separated. The exciting electrodes were then applied respectively to the central ends of the posterior and anterior roots (see fig. 19, *Ex. p.* and *Ex. a.*).

The excitation in the first case invariably evoked a large deflection of the galvanometer, but in the second case *absolutely nothing* even when the secondary coil was brought to 12500 of the Kronecker scale, thus completely covering the primary, *i.e.*, the zero point of the centimetre scale. In other words, the excitatory condition, arriving by the afferent channel or posterior root, not only passed up the few direct fibres of the postero-external, and later of the posterior median column, but probably aroused the afferent portion of the centre from which additional effects might ascend the cord by the internuncial fibres, thus producing a very large deflection in the galvanometer.

On the other hand, the excitatory condition which arrives at the nerve centre by passing up the anterior root or efferent channel is totally unable to reach the afferent side of the centre, and so ascend the cord.

The importance of the negative result of this experiment caused us to vary it as follows :—

In two Cats we divided the posterior roots of the 4th, 5th, 6th, and 7th lumbar nerves and the 1st sacral on the left side. We then divided the cord in the lower dorsal region (10th dorsal), and connected the upper end of the lower fragment with the galvanometer. On exciting the left (mixed) sciatic nerve, which was in connection with the cord by the anterior roots only, no electrical change could be evoked in the observed region of cord however intense the stimulus used, whereas, excitation of only one opposite posterior root gave deflections of 350°, 320°, and with a stimulus of only 500, 130°. This method avoided any chance escape of stimulating current,

which, when this is very intense, might possibly occur in the case of the short anterior root.

These experiments not only illustrate in a very striking manner the extent of the block to the passage of impulses backwards through the efferent side of a spinal

Fig. 19.

nerve centre, they also afford information upon the nature of the anatomical connections of the anterior root fibres with the cord. The histological enumerations of Birge, the developmental researches of His, and the extent of descending degeneration in efferent tracts, have combined to indicate that all the fibres of the anterior roots are in connection with nerve cells lying in the immediate neighbourhood of their

attachment to the cord, and that there are no fibres which pass directly from the columns of the cord (above) outwards into the anterior roots without interruption in a nerve centre. If any uninterrupted fibres exist, then the excitation of the central end of an anterior root ought to give an effect in the galvanometer as arranged in this experiment, for it is well known that the excitatory state (*i.e.*, negative variation) travels indifferently in either direction along continuous tracts. The absence of such effect is a very convincing proof that such through fibres do not exist. Moreover, an additional point receives elucidation from this same experiment. We have already drawn attention to the fact that the anatomical relations of the pyramidal tract fibres are for the most part (and wholly as far as the lower limb is concerned) not with the efferent side of the spinal centres but rather with either the field of conjunction or the afferent aspect.

This anatomical juxtaposition of parts suggests to us that the pyramidal tract fibres for the lower limb do not immediately end in the efferent corpuscles. Such a conclusion is in harmony with the experimental results now under discussion, for it is unreasonable to suppose that the excitatory process would be so entirely blocked when proceeding in the reverse direction along a path consisting merely of two fibres (that of the anterior root and that of the pyramidal tract) joined by a large corpuscle such as one of those in the ventral (anterior) horn.

But we must not anticipate the facts which bear upon the mode of termination of the fibres of the pyramidal tract, and must return to the question of the block offered by the construction of a centre to the passage of nerve impulses.

(2.) *Resistance by the Afferent Side of a Nerve Centre to the Passage of Impulses.*

After having discovered the fundamental position that it is impossible for an excitatory condition to pass "backwards" through a nerve centre from the efferent to the afferent side (whence it could easily spread up the cord), it was clear to us that the next point to be brought into relation with that just described would be the possibility of a nerve centre discharging its energy backwards down an afferent path; or in other words, whether the excitatory condition, if started in the afferent side of a nerve centre, could be transmitted backwards along the posterior roots. Upon this subject we have accumulated a number of facts and experiments from several points of view, and as these are in mutual agreement we can answer the question unhesitatingly in the affirmative.

Many of the facts which establish the conclusion that a spinal nerve centre can and does discharge energy down the posterior as well as the anterior roots when it is stimulated into activity have more important bearings on other questions raised in the present paper, and consequently have been referred to in Chapters VIII. and X. We will, therefore, simply enumerate the facts, and refer the reader to these chapters in which they are described, detailing only those which have not been already treated.

We reserve also to the end of this chapter the pertinent bearing of these observations upon the important doctrine of kinæsthesis (BASTIAN).

The evidence of the passage of nerve impulses, as indicated by electrical changes, from the aroused centres in the cord down the afferent (sensory) fibres of the posterior roots may be grouped as follows :—

(1.) Electrical changes in the posterior roots and mixed nerve with all anterior roots cut when the spinal centres discharge under the influence of strychnia.

(2.) Electrical changes in the above structures when the spinal centres are discharged reflexly.

(3.) Electrical changes in the above structures when the spinal centres are aroused by electrical excitation of the columns of the cord.

(1.) *The Electrical Changes in the Posterior Roots when the Spinal Centres are Excited by Strychnia.*

The most remarkable illustrations of the fact that impulses emerge from a discharging spinal centre on its afferent as well as its efferent side, is that furnished by the following experiments.

In a Cat (211) the cord was divided as usual in the lower dorsal region (11th dorsal) and both sciatic nerves exposed and divided. The central end of each nerve was connected when desired with the galvanometer. The cauda equina was then exposed, and the posterior roots of the 5th, 6th and 7th lumbar nerves, and those of the 1st and 2nd sacral, were divided on the right side, whilst the anterior roots of the same nerves were divided on the left side.

The right nerve was thus in connection with the cord by its anterior roots only, the left by its posterior. Thirty minims of a 1 per cent. solution of acetate of strychnia was now injected intraperitoneally. When the tetanic strychnia spasms commenced, excitatory electrical effects were observed in both nerves.

The amount of the deflections varied with the intensity and direction of the spasms, but were always larger in the right nerve (posterior roots cut) than in the left, averaging 180 in the right, and 30 in the left. The effect, though smaller in the posterior root, was absolutely definite in character, each spasm being accompanied by an effect.

In another animal, Cat (341), we divided the cord at the 12th dorsal vertebra and exposed the cauda equina. We then selected the 7th left lumbar posterior root, divided it near the ganglion and connected in accordance with our method the central end with the galvanometer.

Thirty minims of a 1 per cent. solution of acetate of strychnia were then injected into the peritoneal cavity. Each strychnia spasm caused excitatory electrical effects in the posterior root, which gradually increased in amount in proportion as the discharges became more violent and prolonged. The galvanometer deflections, which were very definite in character and similar in direction to those obtained by the passage of nerve impulses, amounted to 40 at first, then 70, and finally 120.

The employment of clamps, &c., obviated any errors due to the movement of the animal; the experiment may, however, be objected to on the ground that the strychnia discharges are abnormally intense, and must thus break through resistances which ordinary central discharges would be unable to. That the centres can discharge down posterior roots without being under the influence of strychnia is, however, shown by the frequent occurrence of similar though smaller galvanometric effects in the posterior root of an unstrychnised animal, when the cord is discharging in consequence of previous electrical excitation and shallow narcosis.

(2.) *The Electrical Changes in the Posterior Roots when the Spinal Centres are Discharged Reflexly.*

As in the preceding experiments, so here, the evidence is that derived from the electrical changes observed, (*a*) when the posterior root was directly connected with the galvanometer, and (*b*) when the (mixed) sciatic nerve was connected (after division of all anterior roots) with the galvanometer and the central end of one posterior root excited.

(*a.*) In this experiment the central end of one divided posterior root was connected with the galvanometer and the sciatic nerve of the same side stimulated, the result being to produce in the galvanometer a deflection of 20 scale whenever the muscles were thrown into a fair reflex spasm (coil 8000, 341). We shall see presently that this is the amount frequently obtained from the mixed nerve as the result of a reflex discharge. It is most interesting, therefore, to see that the centre reflexly discharges backwards down the posterior root. The bearing of this on the discussion as to which part of a centre is probably the source of the kinetic nerve will be seen further on when this question is raised.

(*b.*) We varied the experiment in another animal, Cat (268), by dividing all the anterior roots supplying the left sciatic nerve and connecting the cut central end of this latter with the galvanometer. We then divided one posterior root, the 6th left lumbar, and excited its central end.

By this arrangement we obtained excitation of the spinal centres in the lumbar enlargement, and at the same time left only the posterior roots or afferent channels for any downward discharge such as would evoke electrical changes in the sciatic nerve.

One observation gave an effect of 10, another of 19 in the galvanometer, the reflex being weak in the first and fairly strong in the second.

(3.) *Existence of Electrical Changes in the Posterior Roots when the Spinal Centres are aroused by Electrical Excitation of the Columns of the Cord.*

The details of these experiments, in which a posterior root was connected directly with the galvanometer and the cut surface of the spinal cord in the dorsal region excited,

are given in Chapter X. Reference to this Chapter will show that the effects in the posterior roots may be due to (*a*) conduction of nerve impulses from the excited area down directly continuous fibres, (*b*) conduction of nerve impulses down fibres which come into relation with cells, and only indirectly with the fibres in the roots. To these two must now be added (*c*) the discharge of impulses from the centres in the cord aroused by the excitation.

It is evident that the discrimination of these different factors can only be achieved by careful comparative experiments made upon the cord, when its direct connections with the roots having been interrupted, the centres are placed under different conditions as regards excitability. These experiments have not as yet been sufficiently satisfactory to enable us to form any decisive opinion on this point.

There is, however, one very important fact already referred to at the close of the preceding Chapter X., to which we must now draw attention.

It will be remembered that, on comparing the results of the experiments detailed in Chapters IX. and X. respectively, the inference was suggested that the indirect channels by which the cord communicates with the posterior roots, are of such a character that they offer more resistance to the passages of impulses from the cord to the nerve than to the passage of similarly evoked impulses from the nerve to the cord. There is thus evidence that, as regards these indirect channels, the same phenomenon of unequal conduction is present which, in its most marked form, exists in the case of the efferent region of the spinal centre.

It must, however, be borne in mind that these indirect channels do not necessarily form the afferent side of the centres, but are only in relation with them, since it is quite possible that in many instances these fibres pass through cells without entering that field of conjunction which forms the *terra incognita* of the centre. Evidence, therefore, of the nature of the discharge from this *terra incognita* backwards down the posterior roots, as well as forwards through the anterior cornual cells, could only be obtained through electrical excitation of the cord, if such excitation was limited to the pyramidal tract. The simplest way of performing this experiment is that of exciting the commencement of this tract in the cortex cerebri, and of observing the changes in the posterior roots. We have endeavoured in two animals to perform this experiment, but without obtaining as yet any satisfactory evidence, nor is this to be wondered at, when it is borne in mind how comparatively small the effects are in the mixed nerve under these conditions.

Summing up the evidence obtained from all methods of experimentation, we are led to conclude that when a spinal nerve centre is thrown into activity, a portion of its energy flows as a discharge backwards down the posterior roots as well as forwards down the efferent fibres of the anterior roots, and upwards and outwards along internuncial fibres to the next centres.

With this somewhat enlarged view of what occurs when a spinal nerve centre

discharges, we will proceed to show what fresh light the galvanometric method is able to throw on the character of the issuing impulses.

Section 3.—Character of Nerve Impulses Discharged by the Spinal Centres.

It seemed to us that an estimate of the amount of the impulses which pass along the nerves as the discharge of a reflex centre, might be obtained by comparing the amount of the electrical change in a peripheral nerve when (*a*) the centre is reflexly aroused, and (*b*) the nerve itself is subjected to a stimulus of similar duration and strength. Such an estimate can only give approximate results, but the difference revealed in the two cases is so striking, and the desired comparison of so much importance in attempting to analyse the components of a reflex, that we have devoted some time to securing it. We have done this for both a "simple" reflex, *i.e.*, that obtained from the same side as that of stimulation, and we have also measured the effect when it is the result of a "crossed" reflex.

(1.) *The Excitatory Electromotive Change Produced in a Mixed Nerve when a Spinal Centre is Excited Reflexly.*

(*a.*) *Simple Reflex.*—To obtain the electrical effect produced by a simple reflex discharge into the peripheral nerves, we divided the spinal cord in the dorsal region, then prepared and divided the sciatic nerve and connected its central end with the galvanometer. The cauda equina was exposed to a limited extent, and a posterior root of the same side selected for excitation; this was divided near the ganglion and its central end stimulated. (See fig. 20.)

The excitation was performed for a known time, as in all our experiments, and the galvanometric effect obtained in the nerve noted. We then applied the same, or a weaker stimulus of the same duration to the observed nerve. The results obtained form a remarkable contrast. The strength of the stimulus is so greatly altered in its effect by the condition of the animal, rest, depth of narcosis, &c., that what is minimal in one case, is quite adequate, or maximal in another.

The readings of the deflections indicating the reflex electrical effects in the nerve were:—

Highest readings	72	60	55	(three highest taken).
Average	26			
Lowest readings	7	3	nil	(three lowest taken).

Out of the whole number of observations, 9 per cent. gave no result. Finally, the stimulus employed on the average amounted to 2500 of the inductorium scale.

Taking the average result, namely, 26 of the galvanometer scale, it is at once

obvious what an extraordinarily small reading this is when compared to that which is observed in a peripheral nerve, or even the peripheral portion of a divided posterior root, which, with a stimulus of one-fifth the intensity (500), and similar duration, averages 227 scale, and once reached a maximum of 445 scale.

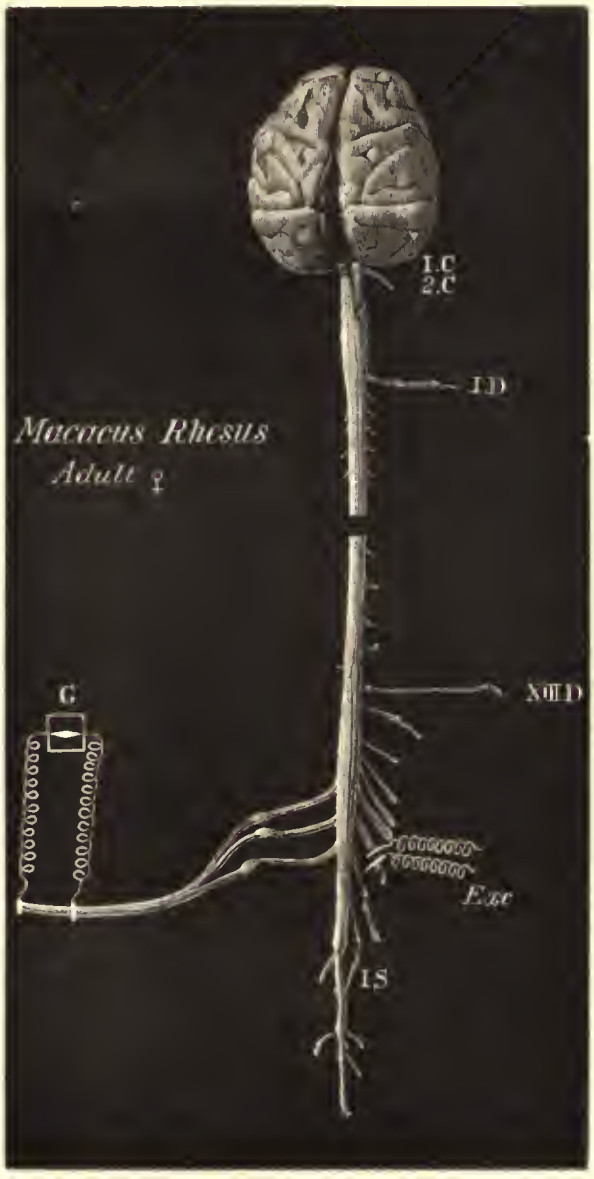
Fig. 20.

This definite result is very significant, but before enlarging upon it we will describe the values obtained for the "crossed" reflex.

(*b.*) *Crossed Reflex.*—To obtain the value of a crossed reflex discharge in the peripheral nerves, we divided, as before, the cord in the dorsal region, and then prepared one sciatic nerve for connection with the galvanometer, and next, either

the opposite sciatic nerve, or corresponding posterior root of the opposite side, for excitation. We made this experiment in nine Cats, two Monkeys, and one Rabbit.

Fig. 21.



The effect in the observed sciatic nerve was, consequently, that due to the discharge of the nerve centres on the side opposite to that of stimulation, or on both sides of the cord.

Owing to the higher excitability of the posterior roots, as compared with that of the mixed sciatic nerve, it is not surprising that we found considerable difference in the amount of effect obtained by crossed reflex action, according as it was

elicited by the one or the other of these two ways. We, therefore, separate the effects into two divisions indicating this difference.

Posterior Root.—The general results in this series of experiments were as follows :—

Effects in nerve by excitation of opposite root.

Highest readings	45	42	42	(three highest taken).
Average	25			
Lowest readings	8	6	nil	(three lowest taken).

These figures are, on the whole, lower than those of the simple reflex. Other considerations emphasise this contrast. These are (1) the proportionate number of cases in which no effect occurred, this being, with the simple reflex, 9 per cent. of the total number of observations, but with the crossed reflex three times as much, viz., 27 per cent. ; (2) the average intensity of the stimulus required to evoke the effect, this being for a simple reflex, an intensity indicated by the secondary coil at 2500, for the crossed reflex the higher intensity indicated by the coil at 3500. Thus, as compared with the simple reflex, the crossed reflex is feebler, less often obtained, and when obtainable requiring a more pronounced stimulus applied to the afferent fibres in a posterior root.

Sciatic Nerve.—In addition to the above we have observed crossed reflex effects which are not comparable with the simple uncrossed effects, since they were evoked by excitation, not of a root, but of the opposite sciatic nerve.

These effects are smaller and more difficult to elicit than those just indicated.

The effects were evoked and observed in precisely the same manner as in the previous cases, and the amounts of the deflections in the central end of the sciatic nerve were as follows :—

Highest readings	20	15	14 (three highest taken).
Average	10		
Lowest readings	6	5	

The intensity of stimulus required to evoke these effects was very much higher than in either of the previous instances, the average being represented by a position of the secondary coil of 8300, whilst it often happened that a position of 12,000 was necessary. It may be remarked that the use of the Helmholtz side-wire in the inductorium minimised any error due to electrotonic escape, such as produces the well-known phenomenon of the so-called " paradoxical contraction."

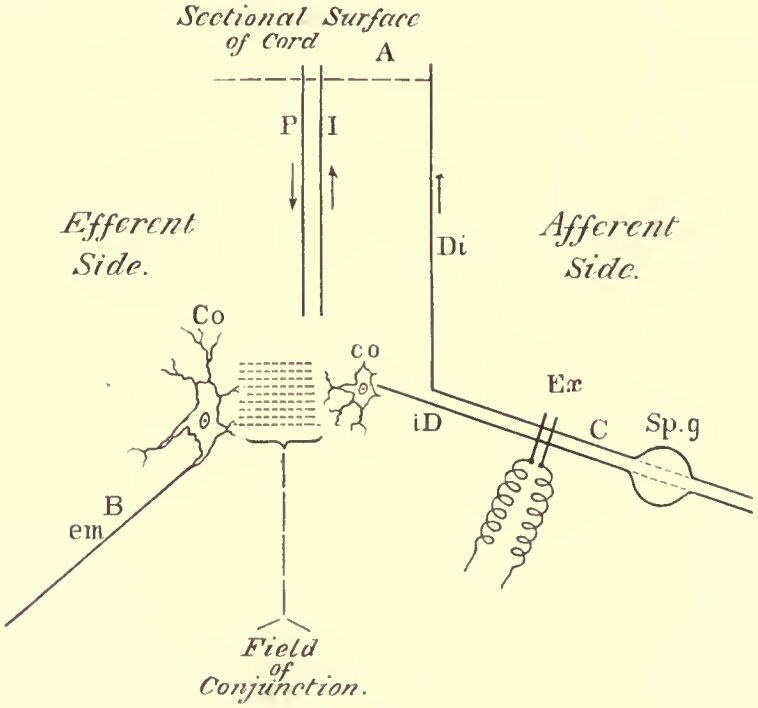
We are now in a position to consider the significance of these results.

The remarkable difference in quantity between the electrical effect in the nerve obtained by exciting the fibres themselves and that which is the result of a reflex discharge from the cord implies that, however intense the excitation of the afferent

side of a centre, the amount of the flow and the intensity of the processes which emerge from the efferent side is small. A comparatively intense excitation is necessary for the etherised centre to discharge at all, and the emerging impulses are so altered in their time relations and intensity, or limited to so few channels, that but little evidence of their presence is indicated by the galvanometric method.

To facilitate further explanations we would call attention to the following diagram, fig. 22, in which are represented the hypothetical elements of a nerve centre.

Fig. 22.



In fig. 22 are shown as simply as possible the three constituent parts of a simple nerve centre, namely, the afferent side, field of conjunction, and efferent side. In addition, the diagram represents the known part of the afferent channel which forms the direct ascending fibres in the spinal cord (Di), the internuncial fibres (I), which also ascend, but which are not yet absolutely known, and the fibres of the pyramidal tract (P).

If a posterior root be excited at the point marked *Ex.* in fig. 22, we can obtain a record of the electrical change evoked by such excitation, in the following parts, namely, the portion of the cord (A) above the excitation, in the outgoing channel (B) (*em.*), and in the channel of excitation (C). On taking the average of all such records we find that they are as follows :—

Average at	A	198.
,,	B	26.
,,	C	250.

Although the cross sectional area of the root is much smaller than that of the cord, yet the effect in the fibres of the root (C) is greater than that in the fibres of the cord (A), suggesting that there is less nerve energy after propagation through the afferent side of the centre. It seemed at first sight not improbable that the effect at A produced by the passage of nerve impulses up the direct channels which join A with C, *plus* additional nerve impulses evoked by a discharge of central activities, would be very large. It would seem, however, if the electrical indications are to be relied upon, and we see no reason to discredit them, that the impulses which enter the central structures from *Ex.* suffer a diminution which more than counterbalances any such addition. We are, however, well aware that the reduction may be due to a spread of nerve impulses in their passage through the afferent side of a centre; and since a similar reduction occurs both in the case of impulses descending the pyramidal tracts, and emerging in the roots, as well as in those which as described are reflex in character, we incline to the opinion that ascending nerve impulses do suffer a diminution in intensity in their passage through the afferent side of a centre.

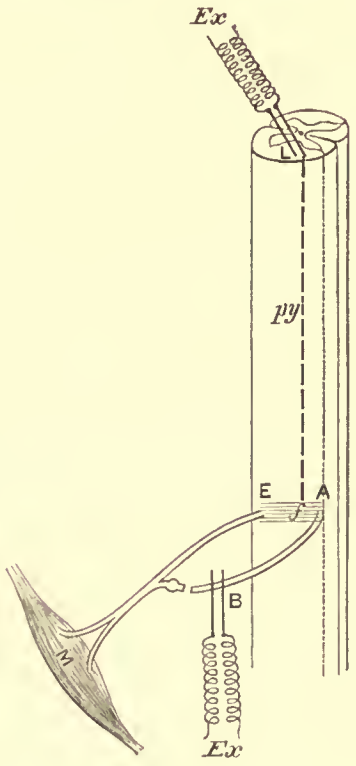
With reference to the impulses descending the pyramidal tracts, whether originating in the cortex cerebri or the fibres of the corona radiata, the facts given in Chapters V. and VI. suggest that a very considerable reduction occurs before they emerge in the anterior roots.

In this connection we would here draw attention to some experiments which we have made to record the muscular contraction evoked by excitation of the spinal centres, and particularly to measure the time between excitation and the commencement of the muscular contraction. The period of delay or latency thus estimated was ascertained by the use of TIGERSTEDT'S signal method, as described in Chapter III., Section 3, and in Chapter VIII., Section 1. In the latter place we have indicated at length the method we employed for the measurement of the rate of transmission of the excitatory effect in the cord fibres, which we found to be about 39·5 metres per second. We have now to point out the reasons which led us to measure the loss of time in a Mammalian spinal nerve centre. It appeared to us that this loss of time which the excitatory condition suffers in going through a spinal nerve centre would not be the same if the path of its entry into the centre is different. There are two modes of entry with which we are familiar. These are (1) the termination of the pyramidal fibres in the nerve centre, (2) the termination of the afferent channels in the posterior root in the nerve centre.

Now, as stated on p. 481, the latter has frequently been estimated, but EXNER has attempted the measurement of the former, and not with a very definite result. These periods of time have not to our knowledge been measured in the Cat, and, as we felt the importance of forming some idea of their value, we performed a few experiments as follows.

The problem in each case is shown in fig. 23. The nerve centre is at EA, E being its efferent, A its afferent side, and f the field of conjunction.

Fig. 23.



The ordinary reflex is produced by the stimulating electrodes being applied to an afferent nerve, the posterior root at B, and the effect recorded by contraction of the muscle M. If the distances BA and EM are known, and the latency delay in the muscle, then it follows that by subtracting these from the total time expended in the execution of the phenomenon we obtain a residue which is the actual delay of transmission of the excitatory effect within the centre EA itself.

This we have done as follows :—

Simple Reflex Delay, two Experiments (Cat).

	Second.
1. Total expenditure of time between excitation at B and contraction at M	·022
2. Time expended in transmission from B to A and E to M at 33 metres per second	·006
3. Time expended in latency of muscle at M	·01

The sum of 2 and 3 gives all the time expended in extrinsic duties ; the subtraction, therefore, of these from 1, gives the delay or loss of time in the centre itself; this amounts to ·006 (in one case ·004).

We now turn to what is more interesting, viz., the loss of time when the impulse

coming to the centre approaches it by way of the pyramidal tract which runs in the lateral column, and is marked as a thick interrupted line in the diagram and by the letters *py*.

To obtain the time loss we have as before to take the total time expended from the moment of excitation at L to that of the contraction of the muscle M, and then to subtract from it the time occupied in simple transmission along the line L*f*M, and, finally, to subtract the latency time of the muscle. These times are as follows :—

DELAY in the Spinal Centre during Excitation of the Lateral Column.

	Average of four experiments (Cats). Second.
1. Total expenditure of time from L to M	·0176
2. Time expended in transmission from L to *f*, and E to M	·006
3. Time expended in latency of muscle	·01

On subtracting 2 + 3 from 1, we get as a final result ·0016. This resultant loss of time is thus several thousandths of a second shorter than the delay taken by transmission of the reflex effect. This is naturally to be expected as a consequence of the lesser amount of centre to be traversed, but possibly the smaller result is also due to the channel of the pyramidal path in the nerve centre being "polarised" for descending and efferent impulses.

It appears, therefore, that when the impulses have to pass through the whole central structure (as in reflex) they suffer both a delay in time and a very marked reduction in quantity, and that when they pass through a portion which excludes the afferent commencement of the centre (cortical discharges), although the reduction is very considerable, the delay is much less.

There is one point to which it is necessary to draw attention before leaving this part of the subject, namely, the well-known susceptibility of central mechanisms to changes from fatigue, these altering the amount of nerve energy discharged. It will be sufficient here to indicate by two examples the influence which previous activity has upon the amount of nerve energy reflexly discharged from a spinal centre, the latter being indicated by the electrical effect in the issuing nerves.

EFFECT of an Interval of Rest on the Simple Reflex Discharge.

	Galvanometric deflections.	
	Before rest.	After rest of 15 minutes.
Excitation of the central end of the left 7th lumbar posterior root gave in the left sciatic nerve	16	42
Excitation of 1st sacral as above	20	39

EFFECT of Want of Rest on the Simple Reflex Discharge.

Cat (263) Excitations following at two minutes' interval of right 7th lumbar posterior root gave in the right sciatic nerve . . . . . :

18	Coil 2000
15	„ 4000
After 15 min. rest	
12	„ 2000
17	„ 4000

Cat (378) Excitations following each other at 1 minute's interval:

26	Coil 2000
8	„ 4000
31	„ 8000
8	„ 8000

Character of the Electromotive Change which is Produced by the Discharge of a Nerve Centre as Contrasted with that Artificially Induced in a Nerve Channel, i.e., Fibres.

The galvanometric method appears to us to suggest differences between the passage of the nerve excitatory condition (so called "nerve impulses") along fibres according to whether it is a centre which is the source, or an artificial stimulus in the actual course of the fibres. Thus, if a peripheral nerve be excited directly by any form of excitation, *i.e.*, electrical or mechanical, the effect in the nerve (*i.e.*, the excitatory condition) shows itself in the galvanometer as a movement which begins sharply and proceeds moderately rapidly, but steadily, so long as the excitation lasts, stopping when the stimulus is left off; upon which return of the needle to zero begins.

It is quite otherwise when the effect in the nerve is due to the passage of the excitatory condition (the "discharge") from a nerve centre. When this latter is excited and the electrical change in the efferent path observed, it shows itself as a slowly developed deflection which gains speed as it moves, does not stop immediately when the stimulation is left off, and only slowly returns towards zero, which it frequently does not completely reach. This peculiar character of the deflection movement is special and easily recognised. If the activity of the centre be impaired, *e g.*, by cooling, drying, &c., the movement is still more sluggish, and is perhaps of more interest; it is *late* in development, *i.e.*, does not commence for one or two seconds after the excitation has begun.

A similar increase of the normal latency in the discharge of the cord, we have also observed by the graphic method, and delay of the kind is frequently noticed in the cortex cerebri (François Franck) when its activity is depressed by any of the agencies referred to on p. 483.

Section 4.—The Influence Exerted by its Central Attachments upon the Electrical Changes evoked in a directly Excited Nerve.

We found, in the course of our experiments upon the nerve roots, that the amount of the electrical change in the nerve evoked by direct excitation of its fibres in any root, varied with the condition of the nerve centres, and was always less when the root was cut away from its central attachments.

We, therefore, designed a series of experiments to test the extent of this influence in the case of the anterior and posterior roots respectively.

This series of experiments consisted in the exposure of the cauda equina, after division of the spinal cord in the dorsal region, connecting the central end of the cut sciatic nerve with the galvanometer, and then raising the posterior roots *seriatim*, and exciting each with the platinum electrodes under all the precautions stated in Chapter III., Section 4. After measurement of the effect observed in the nerve to follow excitation of any posterior root in continuity with the spinal cord, the root was divided about its middle and the peripheral end gently ligatured, raised in the air and excited. The resulting electrical change or effect in the nerve was noted and compared with that obtained from the root when first excited in continuity with the cord.

In every case a diminution was observed in the effect as a direct consequence of severing the peripheral portion from the central apparatus. We feel justified in attributing this change to the cause assigned since the immediate local effect of the section on the peripheral fibres would be to raise rather than depress their excitability. The result, if marked, although conceivably due to the depressing effects of injury, is possibly associated with a loss of a beneficial (nutritive ?) influence derivable from the spinal centres. The deflections observed were as follows :—

Averages.

Posterior root excited.	Effect in nerve.	
	Root excited in continuity with cord.	Root cut and peripheral end excited.
6th lumbar	267	227
7th lumbar	259	172
1st sacral	212	75

Averaging all the observations together, we find that the excitatory effect observed in the nerve, when the uncut root was excited, amounted to 237 scale, whereas that evoked by stimulating the peripheral end was 152 scale. The reduction amounts roughly to about 30 per cent. of the original value, and is especially marked only in the

Fig. 24.

case of the posterior roots. This fact led us, at first, to believe that when a posterior root was excited in its continuity, the spinal centre being of necessity aroused, there must be a flow of energy from the latter down the root, and that this would provide the greater effect noted. This view, however, was materially shaken by the small amount of the reflex discharge obtainable from a nerve centre. We, therefore, regard

the phenomenon from the more general point of view expressed above until further research shall make the question clearer.

Meanwhile in this place we wish to add a few remarks on a curious result which we occasionally obtained (and the meaning of which is very doubtful) by varying the above-mentioned experimental procedure.

As before, we connected the sciatic nerve with the galvanometer, and exposed the cauda equina after section of the cord in the dorsal region. Each posterior root was now excited in continuity with the cord, *seriatim*. The anterior roots were then cut, and the excitation repeated.

In this preparation, therefore, we had the arrangement indicated in the diagram. (Fig. 24.) The first experiment of the kind was simple and uncomplicated, and may therefore serve as an example.

CAT (177). Sciatic Nerve and Roots of the Right Side prepared after Section of the Cord in the Dorsal Region.

Time.	Excitation.	Duration of same.	Posterior root excited in continuity.	Deflection, galv. scale.	Reflex action as observed in muscles.
12.26	4000	5 seconds	7th lumbar	70	Good reflex action
12.31	,,	,,	1st sacral	46	,, ,, ,,
12.39	,,	,,	6th lumbar	62	
12.45	Anterior roots of the above numbers divided.				
12.50	4000	5 seconds	7th lumbar	380	Very vigorous reflex, much more than before
12.53	,,	,,	1st sacral	240	,, ,, ,,
12.55	,,	,,	6th lumbar	280	,, ,, ,,

It will thus be seen that section of the anterior roots seemed to enormously increase the effect in the nerve. We were quite at a loss to understand this result and therefore repeated the experiments. We then found that this striking difference was not always obtainable. In one experiment, for example, in which the section of each anterior root alternated with excitations of the corresponding posterior root, the rise of effect was only noted with one root—viz., the 7th lumbar—in which the effect mounted from 130 to 160, 147, 250, whereas the other roots showed no rise. In this experiment we noted that there was cooling of the preparation, especially of the lower roots. In a succeeding experiment (Cat, 182) we found that warming the cord had a very noteworthy effect on the result, whereas warming the root had not. We then made a fourth experiment (Cat, 268), in which the arrangement of the first was more closely adhered to

CAT (268). Influence of Section of Anterior Roots on the Excitatory Effect in the Nerve, when one Posterior Root is excited in continuity.

Time.	Excitation.	Duration.	Root excited.	Deflection.	
12.3	1000	3·5 seconds	7th lumbar posterior, in continuity	230	Average of two observations
12.6	2000	,,	,, ,,	275	
12.10	Section of the anterior roots of the 5th, 6th, and 7th lumbar, and 1st and 2nd sacral.				
12.20	1000	,,	,, ,,	245	Average of two observations
12.25	2000	,,	,, ,,	320	
	Section of the 6th lumbar and 1st sacral posterior roots.				
12.38	2000	,,	,, ,,	292	
12.46	2000	,,	,, ,,	310	

On summing up these experiments it is evident that the division of the anterior roots does raise the value of the effect in the sciatic nerve evoked by excitation of a posterior root in continuity. In the last three experiments that rise is not so greatly marked as to be more than the supplementary discharge of the spinal centres might account for, but this, of course, does not explain the high readings in the first case.

SECTION 5.—THE SPREAD OF REFLEX DISCHARGES UP AND DOWN THE CORD (INTERNUNCIAL FIBRES).

We have frequently spoken of the existence of internuncial fibres connecting the various centres. It must, however, be confessed that the evidence of their existence is founded almost entirely upon our knowledge of the laws of reflex spread as stated by PFLÜGER. (See Section 1, p. 484.)

We endeavoured to ascertain what light the present galvanometric method would throw upon this spread, and thus upon the localisation and characteristics of these paths. To elucidate this we made a series of experiments in which the cord was excited and the electrical changes noted at the same time that the muscular movements were either recorded or carefully observed.

(1.) *Ascending Discharges (Reflex).*

In the case of reflex discharges it is possible, after division of the cord, to observe the electrical changes in the upper end of the lower fragment of cord, and at the same time to note the contractions of a muscle of the lower (hind) limb.

Since it was desirable to ascertain the relationship between the periodicity of the electrical changes in the cord and that of the muscular twitches, the capillary electrometer was used.

The spinal cord of the Cat being divided in the mid-dorsal region, the upper end of the dorso-lumbar portion was prepared for connection with the electrometer, whilst the lower tendon of the rectus femoris muscle was cut and attached to one of FICK's spring recording levers (isometric method). The cord was then exposed over the dorso-lumbar junction and the lateral column excited with stimuli of varying degrees of intensity. It is obvious that electrical changes thus produced in the cord are due (*a*) to the excitation of continuous fibres joining the excited portion of the lateral column with the observed region, (*b*) to the excitation of indirect fibres in the lateral column, internuncial or otherwise, (*c*) to the discharge of nerve impulses up the cord from the aroused centres.

The main interest of the experiment lies in the fact that with a weak stimulus no muscular effects were observed, although distinct electrical effects were produced; whilst with a strong stimulus the centres in the cord were so aroused that they continued to discharge after the stimulus had ceased, these discharges being evidenced both by muscular contractions and by effects in the electrometer.

The following Table indicates this result :—

EXPERIMENT. Cat (104).—Afferent Effect in Cord compared with Contraction of the Muscle, simultaneously evoked by Intermediate Excitation of the Cord.

Time.	Excitation.	Duration of same.	Effect in cord; electrometer.	Effect in muscle; spring myograph.
4.50	1500	5 secs.	Persistent 2 divs. . .	Nil
4.54	3000	,,	,, 6 divs. . .	Twitch
4.55	4000	,,	,, 7 divs. . .	Initial effect and continued tetanus
4.57	5000	,,	,, 11 divs., followed by intermittent after-effects	Initial characteristic (cord) contraction followed by well-marked after-effect

It is thus seen that when a lumbar spinal centre is aroused to discharge, a flow of nerve energy takes place up the cord as well as out by the efferent roots, and, in all probability, impulses thus pass upwards to various groups of centres both in the upper regions of the cord and in the encephalon.

As to the spinal channels by which these impulses travel,—whether internuncial, direct efferent fibres (pyramidal tract) or direct afferent fibres (posterior column)—the experiment gives no information, and we have not had an opportunity of repeating it on an animal in which, by previous operations, the two latter have been more or less eliminated. Some evidence is afforded by the following experiment, in which the left

posterior column having been divided at the 9th dorsal vertebra, the left 1st lumbar posterior root was excited, and the electrical changes in the cord noted galvanometrically at the same time that the muscular movements were observed.

It will be seen that the electrical change in the dorsal region of the cord was indicated by an effect of 55 in the galvanometer, when the lateral column on the side of the excitation was uninjured; whereas hemisection between the root and the observed region cut down the galvanometric effect to only 7. Before the interruption by the hemisection, a reflex contraction was observed during the excitation in all the muscles supplied by the various nerve segments between the excited root and the observed area of cord, whilst, after the section, such reflex contraction was limited to the piece of cord below the hemisection. The particulars of this second experiment, which appear to suggest that the internuncial fibres are localised in the lateral column, are as follows:—

Cat 376. Cord divided, and peripheral end connected to the galvanometer at the intervertebral disc between the 8th and 9th dorsal vertebræ, section of the *left* posterior column opposite 13th dorsal vertebra.

Time.	Excitation.	Duration of excitation.	Part excited.	Effect in galvanometer.	Effect in neighbouring muscles.
6.3	8000 (Strong stimulus)	5 secs.	Left 1st lumbar posterior root	55	Powerful reflex in trunk muscles

Left hemisection of the cord was then performed at disc between 13th dorsal and 1st lumbar vertebræ.

Time.	Excitation.	Duration of excitation.	Part excited.	Effect in galvanometer.	Effect in neighbouring muscles.
6.12	8000	5 secs.	Left 1st lumbar posterior root	7	Reflex limited to muscles below the point of hemisection

(2.) *Descending Discharges.*

While Pflüger's law concerning the upward internuncial discharge of spinal nerve centres undoubtedly prevails, nevertheless the anatomical investigations of Lockhart Clarke, the physiological observations of Brown-Séquard, and the anatomical researches of Golgi, recently confirmed by Ramon y Cajal, show that there must

be descending channels from at least the afferent sides of the spinal nerve centres, even if there are not direct descending channels. In fact, GOLGI's work goes to show that there are such direct paths, and this is extended by KÖLLIKER. We commenced the investigation of this point by the galvanometric method with an attempt to

Fig. 25.

ascertain whether any electrical change can be detected in the cord below the entry of the stimulated afferent nerve, and have obtained positive results. Our plan was to divide the cord in two places, as in Chapter VIII., and to connect the lower lumbar end of the tract included between the sections with the galvanometer. (See fig. 25.)

The trunk of the last dorsal nerve was then excited.

Cat 378. Cord divided between 8th and 9th dorsal vertebræ, and at dise between 3rd and 4th lumbar vertebræ.

Excitation of left 13th dorsal nerve, effect in lower (lumbar) portion of cord.

Time of observation.	Intensity of stimulus.	Duration of stimulus.	Effect in galvanometer.	Effect in muscles.
		seconds.		
11.33	2000	5	26	Fair reflex
11.36	8000	5	31	Fair reflex

In order to see whether this effect was transmitted by the fibres in the posterior or lateral column, the left posterior column was now divided opposite the centre of the body of the 1st lumbar vertebra. The excitation of the root now gave the following effect :—

Time of observation.	Intensity of stimulus.	Duration of stimulus.		Effect in galvanometer.	Effect in muscles.
		seconds.			
11.58	8000	5	Left 13th dorsal nerve, central end	8	Good reflex
12.4	Left lateral column divided (hence complete left hemisection).				
12.15	8000	5	Left 13th dorsal nerve, central end	6	

We here see most unmistakably that the descending effect is very different in character and localisation from the ascending effect previously described, for (1) it is much smaller, (2) it is mainly dependent upon the continuity of the *posterior* column, whereas the ascending *indirect* effect is dependent upon the integrity of the lateral column.

These results, which were quite unexpected by us, are in very remarkable agreement with the anatomical researches of Golgi, &c.

Section 6.—On the Electrical Changes in the Cortical Nerve Centres.

In all the preceding investigations we have studied the characteristics of a nerve centre by examining the electrical changes, and thus the excitatory processes present in the nerve fibres connected with such a centre. We chose the spinal cord since it contains the simplest form of a complete centre that the Mammalian nervous system presents.

In an early stage of our work the possibility occurred to us of investigating the centres in the cerebral cortex, by the use of the electrical method, this plan having been previously employed by CATON (1875). We selected the occipital lobes (see fig. 26), and endeavoured by stimulation of the retina to obtain evidences of definite

Fig. 26.

electrical changes in the cortex of the moderately etherised Cat, consequent upon the arrival therein of nerve impulses. The difficulties of effectual isolation and the uncertainties of the area of connection, comprising as it does a mass of subjacent nerve fibres, seemed to us to account for the indefinite and capricious character of the electrical indications as displayed by the galvanometer.

The experiments of Beck, of Fleischl von Marxow, and of Danilewsky in this connection have been referred to in Chapter II., which deals with the history of the electrical method. With reference to these we would here only point out that the experiments of Setschenow, Werigo, and ourselves, to which in his Polish paper Beck alludes, seem to us to indicate that the *observed* electrical changes may have their seat in nerve fibres proceeding from or to centres, rather than in any form of central, *i.e.*, corpuscular, nerve mechanism.

Any electrical changes in the contacts of the electrodes with the cortex might, therefore, be as much caused by the impulses travelling in the subjacent fibres as by changes in the cells or other surface termini.

The above criticism obviously does not affect the evidence which the presence of definite electrical changes offers as to localisation, but seems to us to discount any advantage which the method might offer for the investigation of the functions of a nerve centre by the study of the actual changes in its cells.

Summary.

It is obviously impossible to formulate with sufficient accuracy many general conclusions as to the mode in which the functional activity of the spinal nerve centres is generated and discharged, but we cannot refrain from pointing out that the electrical method supplies many ways of investigating this very important and difficult subject, and further that it throws most unexpected light on the obscure questions relating to the working of the several parts of nerve centres.

Most prominently stand out two principal facts :—

(1.) The kinetogenetic portion* of a spinal nerve centre is probably the afferent side. (See Section 2.)

(2.) The part in which the delay and diminution of impulses passing through is effected is the efferent side of such a centre with the field of conjunction. (See Section 2.)

The consideration of these facts, unexpected as they were, shows clearly that the interpretation by Bastian† of sensori-motor nerve phenomena is probably the most correct yet advanced. The basis of that interpretation, namely, the doctrine of kinæsthesis as formulated by him, is in complete harmony with our experimental results.

Bastian has for many years contended that the ordinary division of nerve centres or parts of the same into *sensory* and *motor* respectively is misleading, and that not only has the statement that the source of a nerve centre's discharge is the *motor* part

* By the term "kinetogenetic portion" we have styled that part of a centre in which the potential energy is converted into kinetic.

† "The Brain as an Organ of Mind." "Paralysis, Cerebral, Bulbar, and Spinal."

of it no basis of actual fact, but that it is more philosophical to associate such source with the sensory part.

Among the considerations which favour this view are the following:—The undoubted physiological resemblance which exists between the succession of events in a voluntary or reflex movement, respectively, and the analysis of such psychological events as are known to be concomitants of the former. The psychological phenomena of reflex action show that the afferent impulse in all cases precedes the efferent discharge; psychological analysis also shows that muscular sense impressions similarly precede those discharges which evoke "voluntary" coordinated movements. Hence he concluded that since the sensory excitation always precedes the efferent output, the former must have primary importance, in other words, that the development of kinetic energy must take place in the afferent side of the centre. To express this view briefly he coined the term kinæsthesis.

As the electrical method affords the first opportunity of an experimental contribution to this subject, it is interesting to find how strongly its application bears out BASTIAN'S position. In this chapter it appears probable that the kinetogenetic portion of the centre is the afferent side of it, and the more especially when it is seen how readily the centre discharges into the afferent nerve channels (*i.e.*, actually "backwards," as compared to the course of ordinary afferent impression).

The method has further enabled us to ascertain what connections and facilities for conduction the efferent, or so-called motor side of a nerve centre possesses, and instead of finding, as might have been expected from the ordinarily expressed beliefs on this subject, that we had to deal with a source of energy that was readily aroused, and freely connected with its neighbours, we found, to our surprise, that it afforded nothing of the sort, and that its power of conducting impulses centripetally was apparently *nil*.

Curiously enough, this last point was foreseen also by JAMES, who, in his celebrated work on the 'Feeling of Effort,' 1880, while endorsing the views of BASTIAN, says that the "electrodes of the physiologist," if applied to the central end of the anterior root, would not arouse any "sentient," *i.e.*, afferent impulse in the cord. We are happy to find that our experimental results, unusual though they were, are, nevertheless, in close agreement with the deductions of the logical method of these distinguished writers.

CHAPTER XII.—ON THE ELECTRICAL CHANGES EVOKED IN THE SPINAL CORD AND NERVES BY THE ACTION OF ABSINTHE AND STRYCHNIA.

Section 1.—Experiments (control) including the Use of Absinthe.

Very early in the present investigation on the effects produced by electrical excitation of central apparatuses, the advisability of obtaining a control of our results presented itself. The use of strychnia by du Bois-Reymond as a control demonstration of the excitatory electrical state in nerves, formed, as it always must, the basis of such a method.

We, however, first selected absinthe as particularly exciting nerve centres, and, according to one of us* (V.H.), specially the cortex. Absinthe has been known since the experiments on animals by Marcé† to cause, in small doses, effects only explicable as poisoning of the highest cerebral centres, thus producing mental changes, delirium, hebetude, &c., while in larger doses it evokes clonic epileptiform convulsions with stertorous respiration, &c.

Magnan‡ has, of all writers, contributed the most to our knowledge of the action of this substance.

By injecting small quantities of the essence of absinthe either into the stomach or into a vein, he produced a very striking series of phenomena, which he showed were identical with idiopathic epilepsy.

Following up its action more closely he endeavoured to ascertain the share taken in the production of the fits by the brain and spinal cord respectively. This he investigated by first dividing the cord at the atlanto-occipital articulation, and then injecting absinthe, artificial respiration being kept up.

Unfortunately, he only describes one experiment (No. 6) in which the cord was completely divided. He concludes, however, from his other experiments that the drug excites simultaneously the lower (spinal) and the upper (cerebral) centres. It has, however, been shown by one of us§ that complete section of the cord at the 8th dorsal vertebra prevents the appearance of the characteristic convulsions in the muscles of the parts below the level of the section; and, further, that the corresponding parts or limbs, if the excitable cortex of one side be removed, will not take part in the first general epileptiform convulsions which follow the injection of the drug, whilst, even when in the subsequent fits such parts are affected, the muscles only pass into a slight degree of tonus.

Until a more extended series of researches should negative these points, it is

* 'Brown Lectures.'

† 'Comptes Rendus de l'Académie des Sciences,' vol. 58, 1864, p. 628; also Amory.

‡ 'Recherches sur les Centres Nerveux,' Paris, Manon, 1876.

§ 'Reports of the Brown Institution.'

reasonable to accept the conclusion that absinthe excites *par excellence* the complex cortical centres.

It will be well, perhaps, to mention that by the method of simple observation the following phenomena are elicited by the excitatory action of absinthe.

After injection of two drops of essence of absinthe* into the jugular vein of an animal, narcotised with ether to the degree of unconsciousness, there occur, after a sufficient interval has elapsed (30 seconds or so) to permit of the translation of the poison through the heart and lungs to the arterial system, and so to the brain, the following events :—

The small facial muscles begin to twitch in single clonic spasms, next passing into a state of tremulous tonic spasm. This order of convulsion passes rapidly down the body, until the tonic spasm in the limbs is extremely marked. After this has obtained for a period varying with the dose injected, the tonic spasm gives way to a long series of clonic twitches. Accompanying these motor "discharges," there is profuse salivation, and sometimes escape of urine, while in cases in which narcosis has not been preliminarily employed, unconsciousness and coma are early symptoms.

It is thus obvious that absinthe affords a very simple and efficient means of chemical excitation for the purpose of testing the validity of the results of electrical stimulation of the motor cortex.

We have employed it under the following experimental conditions :—

(1.) Connecting the nerve to the galvanometer or electrometer.

(2.) Connecting the spinal cord to the galvanometer or electrometer, at the same time observing the contractions of the muscles in different parts.

The method employed was, so far as the electrical connections of the observed parts were concerned, precisely that described in the preceding pages. Special precautions had to be taken against any agitation of the preparation. The narcosis with ether being temporarily maintained, the external jugular vein of either side was exposed, penetrated by the needle of a hypodermic syringe, and two minims of the essence of absinthe injected, the narcosis of this drug taking the place of the etherisation, which was forthwith terminated. It was invariably observed that the galvanometer showed evidences of excitatory electrical changes in either nerve or cord, before the muscular contractions in the immediate neighbourhood of the observed level became accentuated.

In respect of what has been said above, we may here add that we never saw contractions of muscles innervated from points below the level of section in the spinal cord when that was divided.

* Obtainable of Messrs. Hopkin and Williams.

(1.) *Excitation of the Intact Central Nervous System by Absinthe.—Electrical Effects in the Sciatic Nerve.*

The results obtained by this arrangement were as follows :—

(*a.*) *Observations with the Galvanometer.*—The experiments were made on four Cats, one to fifteen drops of absinthe being injected. The preliminary effects noted in the galvanometer while as yet the spasms were limited to the upper anterior muscles of the body amounted to small deflections, of which the following are examples : 4, 5, 5, 8, 10, 10, 13, 15.

When, however, the toxic effect of the drug became more marked, and the discharges summated produced a fully developed fit, as above described, then the deflection of the galvanometer was notably increased, and ran up to maxima of 135, 150, 150, 185, 210, 272, 275, these averaging nearly 200. In smaller attacks, but still generalised, the deflection varied from 45 to 85. With regard to the magnitude of these deflections, it is to be noted that their large amounts are doubtless due to the completely bilateral and prolonged character of the cortical discharges and the continued effect on the galvanometer.

(*b.*) *Observations with the Electrometer.*—When during any one of the above observations the electrodes in contact with the central end of the nerve were switched over so as to bring it into connection with the electrometer, the effect was visible, but varied notably in amount from a small movement of the mercurial meniscus to 1 division.

It was thus abundantly clear that the employment of absinthe gave maximal electromotive effects in the sciatic nerve through the overwhelming discharge of the highest cortical centres, and the figures obtained from the galvanometric deflections give a fair notion of the comparative magnitude of these discharges, the more especially as the degree to which the epileptic discharge developed could be plainly seen in the amount and duration of the spasm in the neighbouring muscles. This being so, it is, of course, hardly necessary to add that the cessation of the convulsion was synchronous with a halt in the swing of the galvanometer needle.

(2.) *Excitation of the Nervous System by Absinthe.—Electrical Changes in the Spinal Cord.*

As might have been anticipated, the electrical effects observed in the spinal cord when the central mechanisms were excited by a diffuse stimulus, such as that of absinthe in the circulation, were larger than that witnessed in the peripheral nerve.

We have made four experiments in Cats, and one in the Monkey (*Macacus rhesus*), and have usually measured the effect with the electrometer. With this instrument the excursions of the mercury were very marked, varying from slight movement in the case of initial spasms to excursions of even five divisions in severe fits.

In the galvanometer, similarly, the lowest recorded deflection was 110, the highest being over 300 and obviously conditioned by the duration of the convulsions.

No comparison can be drawn between the magnitude of the deflections and those obtained from the nerve, for the above and other reasons. In general they confirm the validity of the views advanced, respecting the results obtained by electrical excitation of the central nervous system as detailed in the foregoing chapters.

An experiment in this connection may here be mentioned as of special interest regarding the action of absinthe. The toxic action of this drug is unquestionably excitatory as far as the highest nerve centres are concerned. François Franck * found that it produced inexcitability of the cortex. One of us has previously suggested that this is a question of dosage, in common with other narcotic agencies. In the present series, while observing in one case the deflection produced by absinthe, we superadded electrical excitation of the previously exposed cortex. The result (Cat 99) was to notably increase the effect. Thus, while the chemical stimulus was actually evoking a powerful discharge, the additional electrical excitation caused the centres to produce still more kinetic energy. In this stage, therefore, the absinthe had not exhausted the cortex. The additional effect was visible, both in the electrometer and galvanometer, when either was switched on to the cord.

Section 2.—Experiments (control) including the use of Strychnia.

The method of employing strychnia differed from that detailed in the case of absinthe in one important particular, namely, that the spinal cord was severed from its connection with the encephalon. The spinal cord in two Cats and one Monkey, and the sciatic nerves and the posterior root in two Cats, were connected with the galvanometer for observation of the excitatory electrical changes. The solution of strychnia employed was a 1 per cent. solution of the acetate. It was injected into the peritoneal cavity, and the toxic symptoms observed. The tetanic spasms, like those obtained by absinthe, were of very varying force and duration, but gave far higher readings than absinthe. We will return to this point later, and meanwhile briefly state the results obtained.

(1.) *Electrical Effects in the Sciatic Nerves.*—The observation of the effects in the Mammalian nerve during the discharges due to strychnia has furnished valuable control results. We have, however, used the method to obtain by its means the evidence referred to in the preceding chapter on the discharge of a nerve centre backwards down the posterior root as well as the discharge down the anterior roots.

(2.) *Electrical Effects in Posterior Root.*—Similar changes to those in the nerve have been obtained in the case of the posterior root. These have been already referred to in Chapter XI., Section 3.

(3) *Electrical Effects in the Spinal Cord.*—When the spinal cord of an animal was

* *Loc. cit.*

severed, and the lower fragment connected in the manner practised in all the preceding experiments, and strychnia injected, very large electrical changes were observed. These were produced in the upper, as well as the lower, end of the dorso-lumbar portion of the cord. The maximal effects were over 500 scale of galvanometer, and the average in one experiment of all the readings was as high as 300.

To sum up these experiments with a chemical stimulus, from the point of view from which they were designed, it is clear that the excitatory electromotive changes (*i.e.*, diminution in the resting difference) observed to occur in the central nervous system when that is excited electrically or mechanically, are true indications of physiological phenomena accompanying functional activity, and, further, that their amounts vary directly in proportion with the intensity and duration of such activity.

CHAPTER XIII.—SUMMARY AND CONCLUSIONS.

The consideration of the results given in the foregoing chapters shows, we venture to think, that the electrical method of investigating the localisation of nerve impulses in the Mammalian nervous system is one which has furnished several new aspects of nerve function, and we believe that if further pursued it will prove one of the most valuable means of differentiating the structure of the nervous system, and gauging the nature of the functional activity of the nerve centres.

In view of the extended scope of our present research, we feel unable to give a sufficiently brief summary of the results. We therefore propose to enumerate, by way of conclusion, some of the general principles which we think we are justified in deducing from our work.

The following remarks, therefore, cannot in any sense be regarded as embodying the whole of our investigations, and we must consequently refer our readers to the individual chapters, and especially to the remarks at the end of each, for information as to points upon which we do not here touch.

(1.) *Resting Electrical Difference.*

The resting electrical difference between the cut and uninjured longitudinal surface respectively in the Mammalian mixed nerve, spinal nerve root, and spinal nerve, has been found by us to have the following value:—

	Cat.	Monkey.
Nerve	(69 cases) ·01 Daniell	(12 cases) ·005 Daniell
Root	(5 cases) ·025 ,,	
Cord	(50 cases) ·032 ,,	(10 cases) ·022 ,,

We have found, further, that the difference is subject to variations of which the following are the most important :—

(*a.*) A notable fall is observed in all three tissues in consequence of systemic death.

(*b.*) The difference in the cord is increased after the functional activity of the organ has been aroused.

(*c.*) The difference in the cord is more pronounced when the tissue is in connection with the encephalon. (See Chapter IV.)

(2.) *Effect in the Spinal Cord on Excitation of the Cortex Cerebri.*

In extension of our discovery that excitatory electrical effects can be observed in the spinal cord to result from excitation of the cortex cerebri, as previously described, and by means of which the character of the impulses derived from the cortical centres may be studied, we have obtained effects in both the cord and the mixed nerve, following similar excitation of the cortex, and by comparing the result of these observations together have found that the excitatory state evoked by cortical activity undergoes a diminution of over 80 per cent. in the passage from the cord into the sciatic nerve.

We have also applied the galvanometric method to differentiate the cortical excitable areas, by recording and comparing the discharges from the same in the spinal cord, and have found a striking degree of localisation demonstrated thereby in the Cat as well as the Monkey. (See Chapter V.)

(3.) *Effect in the Spinal Cord on Excitation of the Corona Radiata.*

By a comparison made between the amounts of the electrical effects produced in the spinal cord and the mixed nerve respectively after excitation of the corona radiata, we found that the cord effect is four times as great as that in the nerve, and further, that this corona-radiata-to-cord effect is little more than half the complete cortex-to-cord change. (See Chapter VI.)

(4.) *Bilaterality.*

By comparing the records of the extent of the electrical effects in each half of the longitudinally divided cord, and in the mixed nerve of each side, we have made fresh observations on the important and complex question of bilaterality of representation in the central nervous system. We have found—

(*a.*) That it is possible to obtain strictly unilateral effects in both the spinal cord and sciatic nerve with complete excitation of both cortex cerebri and corona radiata.

(*b.*) That the circumstances which favour the production of bilateral effects are such as bring into play other portions of the central nervous system, *e.g.*, the opposite excitable cortex, cerebellum, and basal structures ; and,

(*c.*) That such bilateral effects, under these circumstances, can be evoked more readily by excitation of the corona radiata than of the cortex.

Hence, we conclude that, as far as the cortical efferent representation of the lower limb in the Cat and Monkey is concerned, the normal condition is that of unilaterality. (See Chapter VII.)

(5.) *Electrical Changes evoked in the Spinal Cord by Excitation of its Columns.*

Observation of the electrical changes in the dorso-lumbar spinal cord, when evoked by direct excitation of its fibres after severance from the encephalon, has revealed by comparison of the electrical changes produced the proportionate existence of direct and indirect channels in the various columns of the cord.

We have thus examined the columns so far as they conduct ascending and descending impulses respectively in the Cat and Monkey. This analysis we extended by employing the exclusion method of intervening sections, as an addition to observations on the intact cord. The results show that :—

(*a.*) In the Monkey a relatively larger number of direct fibres are contained in the lateral column than in the posterior column, the reverse being the case in the Cat.

(*b.*) For both classes of impulses and of animals observed we have obtained (α) no evidence of crossing between the lateral columns, (β) evidence of indirect connections between one posterior column and the lateral column of the same side, (γ) evidence of cross connections between the posterior columns.

(*c.*) There is no evidence of the existence in the anterior columns of the cord (Cat and Monkey) of any continuous fibres between the mid-dorsal and lumbar regions.

(*d.*) The spread of impulses from path to path in the spinal cord appears, in addition to what is stated under (*b*), to be conditioned as follows :—The posterior column fibres spread into other columns more as they ascend than as they descend, whereas the fibres of the lateral column spread in a converse manner. (See Chapter VIII.)

(6.) *The Relations of the Spinal Cord to the Lumbar Nerves.*

We have investigated the relation of the peripheral nerves and their roots to the paths and to the bulbo-spinal centres in the dorso-lumbar region of the spinal cord.

The investigations consisted in observing (A) the electrical changes produced by exciting the mixed nerves or their roots in the spinal cord when separated from the encephalon, (B) the electrical changes produced by excitation of the divided cord in the spinal nerves, and (C) the excitatory changes produced by stimulation of the spinal centres.

A. The results obtained by the first method may be grouped as follows :—

(*a.*) By far the majority of afferent impulses ascend the cord on the same side as

the entering root, both by direct and indirect paths, a small minority ascend by the posterior column of the opposite side, and a mere fraction by the lateral column of the opposite side.

(*b.*) The direct path of afferent impulses is localised in the posterior column of the same side as that of the nerve or root excited.

(*c.*) The indirect paths of afferent impulses are localised in the posterior columns of both sides, and in the lateral column of the same side as that of the excited nerve.

(*d.*) The proportionate development of both systems of nerve paths in the two sides of the cord may be inferred from the percentages of the total transmission of excitatory electrical changes from the afferent nerve to the cord.

Of the electrical changes there are transmitted by :—

		Same side.
Posterior column of same side as excited nerve . .	60 per cent.	80 per cent.
Lateral „ „ „ „ . .	20 „	
		Opposite side.
Posterior column of opposite side to „ . .	15 „	20 per cent.
Lateral „ „ „ „ . .	5 „	

(See Chapter IX.)

B. The descending electrical effects, as far as the relationship of the cord and nerves is concerned, were investigated in the mixed nerve, the spinal cord being severed from the encephalon and excited.

The results of these experiments, obtained with both minimal and maximal stimuli, and controlled by the exclusion method of intervening sections, were as follows :—

(*a.*) On minimal excitation of the posterior column, impulses are directly transmitted into the posterior roots of the same side, and so into the mixed nerve ; with maximal excitation some impulses are similarly transmitted through indirect paths.

(*b.*) On maximal excitation of the posterior column, impulses are transmitted by indirect paths across to the posterior roots of the opposite side, and so to the mixed nerve of that side.

(*c.*) On excitation of the lateral column, impulses are indirectly transmitted to the mixed nerve of the same side as that of the excited column.

(*d.*) The proportionate percentage of the total transmission of excitatory electrical states from the various excited columns of the dorsal cord into the mixed nerves is as follows :—

				per cent.		per cent.
Excitation of	posterior column	of same side as	observed nerve	73	Same side	82
„	lateral	„	„	9		
„	posterior	„	opposite	15	„	18
„	lateral	„	„	3		

(*e.*) Our evidence shows that electrical states (*i.e.*, impulses) are transmitted with great facility from the excited areas in the cord down the afferent channels of the cord, posterior roots, and nerves (see Chapter X.).

C. The researches into the relationship between the spinal cord in the dorso-lumbar region and the mixed nerve and spinal nerve roots, have enabled us to formulate some generalisations on the functional activity of the spinal nerve centres as follows :—

(*a.*) There is complete obstruction to all centripetal impulses which may reach the cord by the central end of the anterior root.

(*b.*) A marked quantitative diminution as well as delay in time is suffered by impulses which leave the spinal cord by the anterior roots, whether these have originated in the cortex cerebri, corona radiata, or the lateral columns of the cord.

(*c.*) An increased resistance to descending, as compared to ascending, impulses by certain indirect paths is offered connected with the afferent side of the spinal centres.

(*d.*) Whenever a spinal centre discharges, nerve impulses pass from it down the posterior roots as well as the anterior.

(*e.*) The effect produced in a mixed nerve by the reflex discharge of a spinal centre down the nerve fibres is notably small when compared with that evoked by their direct excitation (see Chapter XI.).

It will be gathered from the extent and variety of the above conclusions that the employment of the method used in the above research has led us on from one investigation to another. We commenced our experiments with the object of ascertaining the character of the cortical discharge, and we employed for this purpose the capillary electrometer.

We then made use of the galvanometer for the same purpose, and at once found that a method was opened up for investigating, not merely the general characters of a cortical discharge of impulses, but the comparative amounts of such impulses when generated in different parts of the Mammalian nervous system. This led to its employment as a means of ascertaining the distribution of the channels in the spinal cord along which these impulses passed, and thus to the determination of the extent to which afferent as well as efferent nerve impulses were localised in fibres on one or the other side of the cord. The necessity of stimulating for this purpose the various roots of the nerves brought before us in a most striking manner the remarkable difference between the central connections of the two kinds of roots, and thus finally opened up the possibility of new investigations into the anatomical relations of a centre and the particular physiological attributes which characterise it.

The correctness of the method is, we think, shown by the way in which the results set forth in the foregoing chapters were progressively obtained by its use. Many of them were unexpected by us, and needed ample verification. We had thus an opportunity, in frequent repetition of the same experiment, of probing the extent to which the data our method furnished could be relied upon. From this point of

view we are firmly convinced that, when proper precautions are used to avoid the disturbing influence of capricious factors, the present plan is one which gives as sure indications as any other method which has been used in the carrying out of investigations into the central nervous system, whilst by its mode of application it has the merit of ensuring definite localisation in hitherto unexplored regions. The wide extent of the field of research which the use of the method opens up is obvious. We have only employed it for elucidating a few of the phenomena which are exhibited by the functions of the brain and spinal cord; but the functions of various ganglia, the relations of the sympathetic system, of the more central portions of the bulbo-spinal system, and finally of the encephalic structures may, and undoubtedly will, be satisfactorily approached in the future by its means.

Appendix A.—Topographical Relations existing between the Superficial Origins from the Spinal Cord of the Spinal Nerves, and the Bodies of the Vertebræ in the Cat.

Cervical Nerve.	Corresponding Vertebræ.
I.	Upper border of 1st cervical
II.	Upper half of 2nd cervical
III.	Middle of 3rd cervical*
IV.	Upper border of 4th cervical*
V.	Intervertebral disc between 4th and 5th cervical
VI.	Lower border of 5th cervical and disc between 5th and 6th cervical
VII.	Lower half of 6th cervical
VIII.	Centre of 7th cervical
Dorsal.	
I.	Disc between 7th cervical and 1st dorsal
II.	Lower border of 1st dorsal and disc between 1st and 2nd dorsal
III.	Lower half of 2nd dorsal
IV.	Lower half of 3rd dorsal
V.	Lower two-thirds of 4th dorsal
VI.	Centre of body of 5th dorsal
VII.	Lower half of 6th dorsal, and disc between 6th and 7th dorsal
VIII.	Lower half of 7th dorsal, and disc between 7th and 8th dorsal
IX.	Disc between 8th and 9th dorsal
X.	Intervertebral disc between 9th and 10th dorsal
XI.	Upper half of body of 11th dorsal
XII.	Middle of body of 12th dorsal
XIII.	Lower half of body of 13th dorsal
Lumbar.	
I.	Lower half of 1st lumbar, and disc between 1st and 2nd lumbar†
II.	Lower quarter of 2nd lumbar, and disc and upper quarter of the 3rd lumbar centre opposite disc†
III.	Disc between 3rd and 4th lumbar
IV.	Lower border of 4th lumbar
V.	Middle of 5th lumbar
VI.	Lower quarter of 5th lumbar and disc between 5th and 6th
VII.	Upper fourth of 6th lumbar
Sacral.	
I.	2nd fourth of 6th lumbar
II.	3rd fourth of 6th lumbar
III.	Disc between 6th and 7th lumbar

Coccygeal.—The cord tapers gradually to 3rd sacral vertebra.

* These nerves consequently run slightly forwards from the cord to leave the intervertebral foramina.

† These nerves are directed slightly forwards on leaving the cord.

APPENDIX B.—Table showing Persistent Electrical Difference between Surface and Cross Section. Distance between Contacts 1 centim. Difference expressed in fractions of 1 Daniell.

I. SCIATIC NERVE.

(1) *In Connection with Brain.*

Cat (71)*	·018
„ (73)	·013
„ (75)	·018
„ (166)	·008
„ (273)	·009
„ (288)	·008
„ (290)	·009
„ (291)	·004
„ (292)	·006
„ (301)	·004
„ (301)	·006
„ (296)	·009
„ (296)	·008
„ (298)	·01
„ (298)	·009
„ (299)	·009
„ (299)	·013
„ (303)	·009
„ (305)	·009
„ (305)	·01
„ (382)	·009
„ (384)	·0075

Average ·0094 Daniell.

Monkey (47)	·007
„ (217)	·005
„ (217)	·006
„ (221)	·005
„ (221)	·006
„ (262)	·003
„ (270)	·003
„ (280)	·004
„ (333)	·005
„ (333)	·006
„ (368)	·005
„ (368)	·007

Average ·005 Daniell.

(2) *Cord Divided in Dorsal Region.*

Cat (32)	·005
„ (36)	·007
„ (36)	·007
„ (157)	·009
„ (161)	·011
„ (164)	·009
„ (168)	·008
„ (172)	·012
„ (173)	·011
„ (175)	·007
„ (177)	·008
„ (179)	·008
„ (181)	·011
„ (190)	·01
„ (200)	·008
„ (201)	·011
„ (203)	·007
„ (204)	·008
„ (363)	·009

Cat (64)	·012
„ (65)	·013
„ (206)	·01
„ (209)	·012
„ (209)	·01
„ (254)	·011
„ (263)	·009
„ (265)	·008
„ (267)	·006
„ (267)	·007
„ (275)	·0085
„ (276)	·0125
„ (311)	·0125
„ (312)	·012
„ (329)	·01
„ (329)	·012
„ (331)	·008
„ (331)	·011
„ (363)	·007

Average ·0094 Daniell.

* As stated on p. 303, the numbers in brackets following the mention of an animal refer to the page in our note ledger in which the observation is recorded.

(3.) *After Previous Operations on Cord.*

Cat (227) division of left posterior roots . . . . . ·007 left
„ (227) „ „ „ . . . . . ·009 right
„ (230) division of right posterior column . . . . ·008 left
„ (230) „ „ „ . . . . ·005 right
„ (247) „ „ „ . . . . ·012 right
„ (251) division of both posterior columns . . . . ·012 right
„ (259) left hemisection . . . . . ·009 left
„ (259) „ . . . . . ·008 right

II. Lumbar Roots.

7th Left Lumbar Posterior Root.

Cat (341) . . . . . ·026
„ (348) . . . . . ·02
„ (362) . . . . . ·02
Cat (381) . . . . . ·018
„ (382) . . . . . ·016
Average ·02 Daniell.

6th Lumbar Posterior Root.

Cat (383) . . . . . ·011

6th Lumbar Anterior Root.

Cat (383) . . . . . ·0045

III. Spinal Cord.

Electrical Difference between Cross Section and Surface. Cord Divided and Isolated at Position Indicated in Table. Contacts 1 centim. apart.

(1.) *Cord in Connection with Brain*

Cat (51) 1st lumbar . . . . ·033
„ (80) 12th dorsal . . . . ·044
„ (97) 12th dorsal . . . . ·03
„ (114) 2nd lumbar . . . ·037
„ (118) 4th lumbar . . . . ·04
„ (124) 3rd lumbar . . . . ·046
„ (126) 2nd lumbar . . . ·04
„ (288) 13th dorsal . . . . ·033
„ (308) 1st lumbar . . . . ·033
„ (314) 12th dorsal . . . . ·025
„ (315) 13th dorsal . . . . ·032
„ (317) 13th dorsal . . . . ·032
„ (319) 12th dorsal . . . . ·029
„ (323) 13th dorsal . . . . ·031
„ (324) 13th dorsal . . . . ·033
Average ·034 Daniell.

Monkey (41) 12th dorsal . . . ·018
„ (48) 12th dorsal . . . ·024
„ (52) 12th dorsal . . . ·029
„ (54) 12th dorsal . . . ·027
„ (234) 12th dorsal . . ·025
Average ·025 Daniell.

(2.) *Cord Severed from Brain.*

Cat (37) 8th dorsal	·043
„ (67) 9th dorsal	·026
„ (100) 9th dorsal	·036
„ (104) 9th dorsal	·03
„ (121) 11th dorsal	·031
„ (140) 10th dorsal	·03
„ (145) 10th dorsal	·03
„ (148) 11th dorsal	·025
„ (151) 10th dorsal	·035
„ (153) 11th dorsal	·025
„ (192) 11th dorsal	·023
„ (194) 10th dorsal	·018
, (196) 10th dorsal	·03
„ (243) 8th dorsal	·025
„ (255) 8th dorsal	·03
„ (289) 7th dorsal	·014
„ (327) 9th dorsal	·028
„ (337) 6th dorsal	·026
„ (339) 8th dorsal	·03
„ (344) 8th dorsal	·04
„ (346) 8th dorsal	·026
„ (349) 10th dorsal	·02
„ (355) 8th dorsal	·04
„ (375) 8th dorsal	·039

Average ·029 Daniell.

Monkey (271) 8th dorsal	·017
„ (281) 8th dorsal	·027
„ (321) 7th dorsal	·013

Average ·019 Daniell.

Cat (37) 2nd lumbar	·035
„ (124) 4th lumbar	·033
„ (170) 1st lumbar	·029
„ (243) 2nd lumbar	·033
„ (301) 1st lumbar	·037
„ (357) 2nd lumbar	·036
„ (366) 2nd lumbar	·033
„ (371) 1st lumbar	·03
„ (378) 3rd lumbar	·028

Average ·033 Daniell.

Monkey (321) 2nd lumbar	·018
„ (232) 2nd lumbar	·018

(3.) *Cord in Connection with Brain, but divided Longitudinally into Right and Left Halves.*

		Left.	Right.
Cat (129)	2nd lumbar	·029	·018
„ (130)	1st lumbar	·01	·014
„ (133)	2nd lumbar	·028	·021
„ (135)	3rd lumbar	·022	·019
„ (309)	1st lumbar	·018	·027
„ (318)	13th dorsal	·018	·019
„ (324)	13th dorsal	·015	·022

Average ·02 and ·02 Daniell.

		Left.	Right.
Monkey (213) .	10th dorsal . . .	·02	·014
,, (215) .	10th dorsal . . .	·023	·012
,, (217) .	11th dorsal . . .	·013	·011
,, (235) .	11th dorsal . . .	·013	·011
,, (237) .	2nd lumbar . . .	·013	·009
Average ·016 and ·011 Daniell.			

(4.) *Cord Severed from Brain and Divided Longitudinally.*

		Left.	Right.
Cat (137) . . .	8th dorsal . . .	·007	·016
,, (143) . . .	9th dorsal . . .	·021	·013

(5.) *After Section of Columns 1–3 Months Previous to Observation. Cord Severed from Brain.*

Cat (228) division of posterior roots on one side, 11th dorsal . . . . . ·012
,, (231) division of right posterior column at 7th dorsal, 11th dorsal . . ·025
,, (252) division of both posterior columns at 10th dorsal, 6th dorsal . . ·022
,, (260) left hemisection at 9th dorsal, 4th dorsal . . . . . ·017
,, (283) left hemisection at 12th dorsal, 6th dorsal . . . . . ·038
,, (228) hemisection on right side at 9th dorsal, 1st lumbar . . . . . ·018
Average ·022 Daniell.

(6.) *General Average.*

Average, all cases, cord, Cat . . . . . ·032 Daniell.
,, ,, Monkey . . . . ·022 ,,

Description of Plates 29–35

Plate 29. Arrangement of an experiment on a Cat for the investigation of electrical changes in the spinal cord consequent upon excitation of the peripheral nerves. See Chapter III.

Plate 30. Photograph of the encephalon and spinal cord of an adult Cat, two-thirds natural size, showing correctly the proportionate size of the various regions of the neural axis.

The spinal nerves in this and the succeeding Plates are indicated by Roman figures and capital letters.

a, *b*, *c*, *d* are points on the cortex cerebri referred to on page 329.

Plate 31. Photograph of the neural axis in a Cat; the same preparation as in Plate 30, as arranged for the experiments on bilaterality, &c.

Plate 32. Photograph of the encephalon and spinal cord of an adult Rhesus Monkey, to show, in comparison with Plate 30, the proportionate size and details of the neural axis in the Monkey as contrasted with the Cat.

Plate 33. Photograph of the neural axis in the Monkey; the same preparation as in Plate 32, as arranged for the experiments on bilaterality, &c.

Plate 34. Photograph of a recent dissection of the lumbar plexus in an adult Monkey, showing the arrangement of the roots entering the plexus.

A.c. = Anterior crural nerve.
Ob. = Obturator nerve.
E.P. = External popliteal.
I.P. = Internal popliteal.
IIs. = Branches to hamstring muscles.
An. = Branches to anal and pudic plexuses.
* = Filum terminale.

Plate 35. Photograph of a recent dissection of the lumbar plexus in an adult Cat. Lettering as in Plate 34.

S.s. = Small sciatic.

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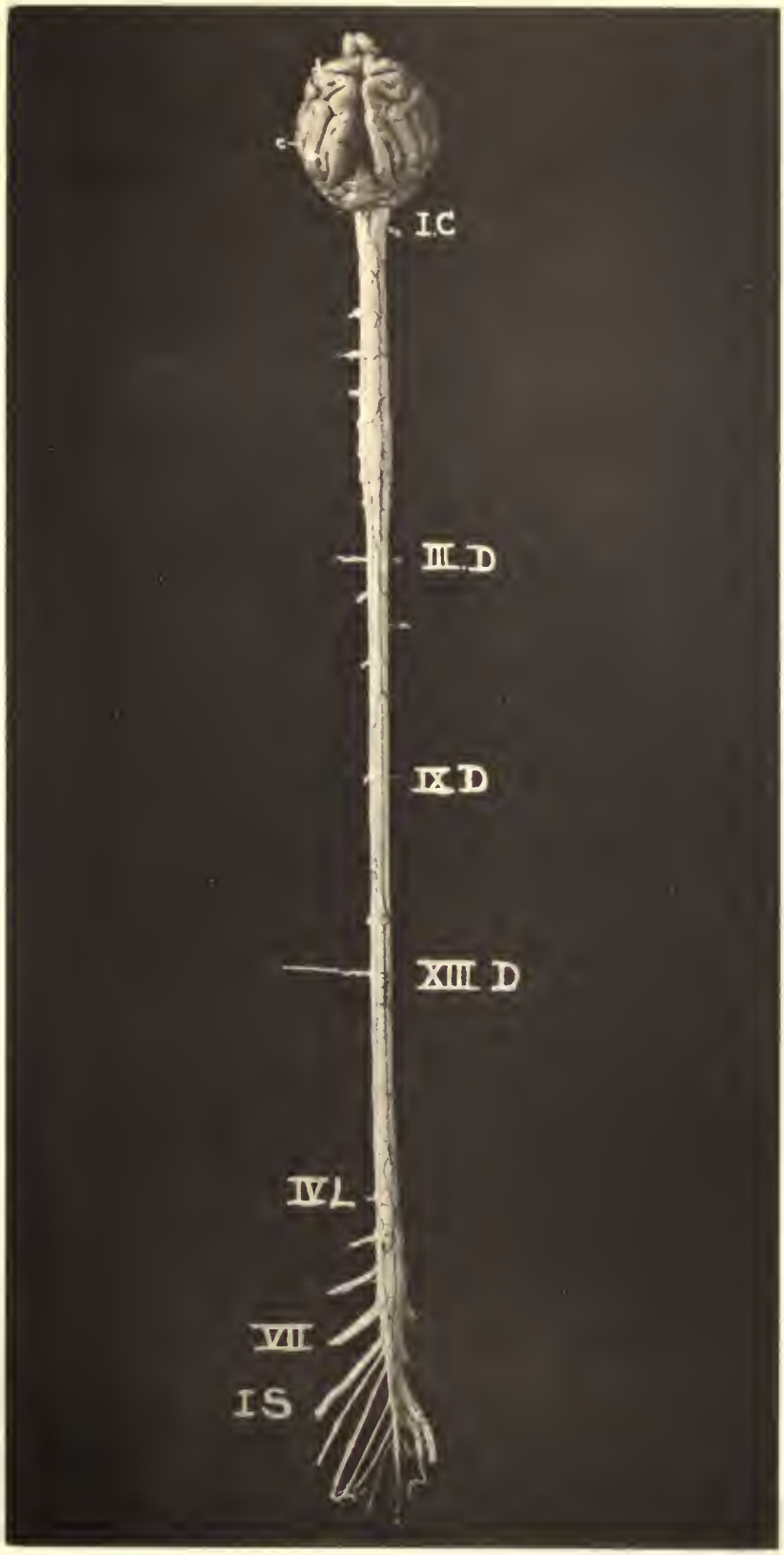

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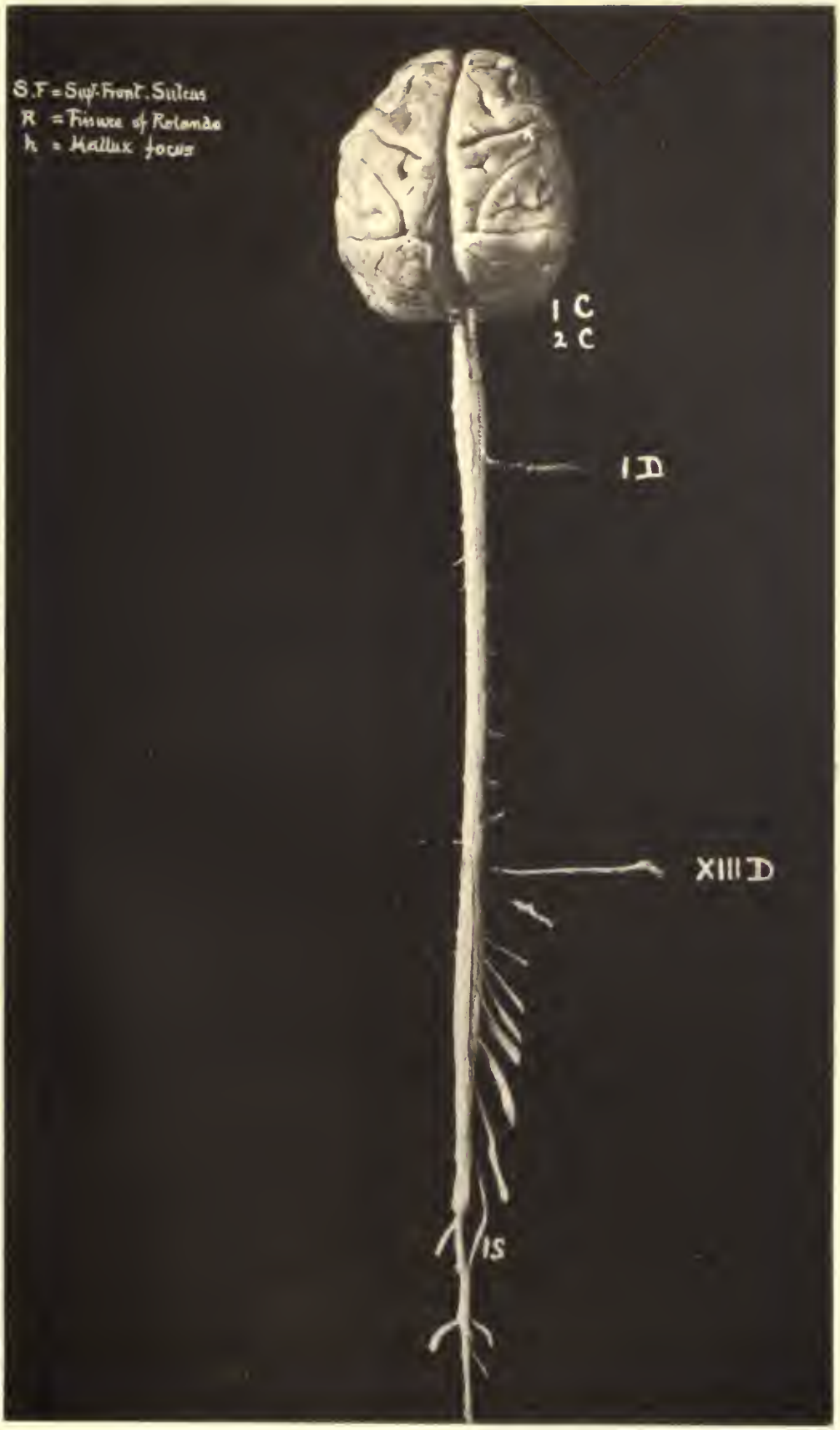
CAT ADULT ♀



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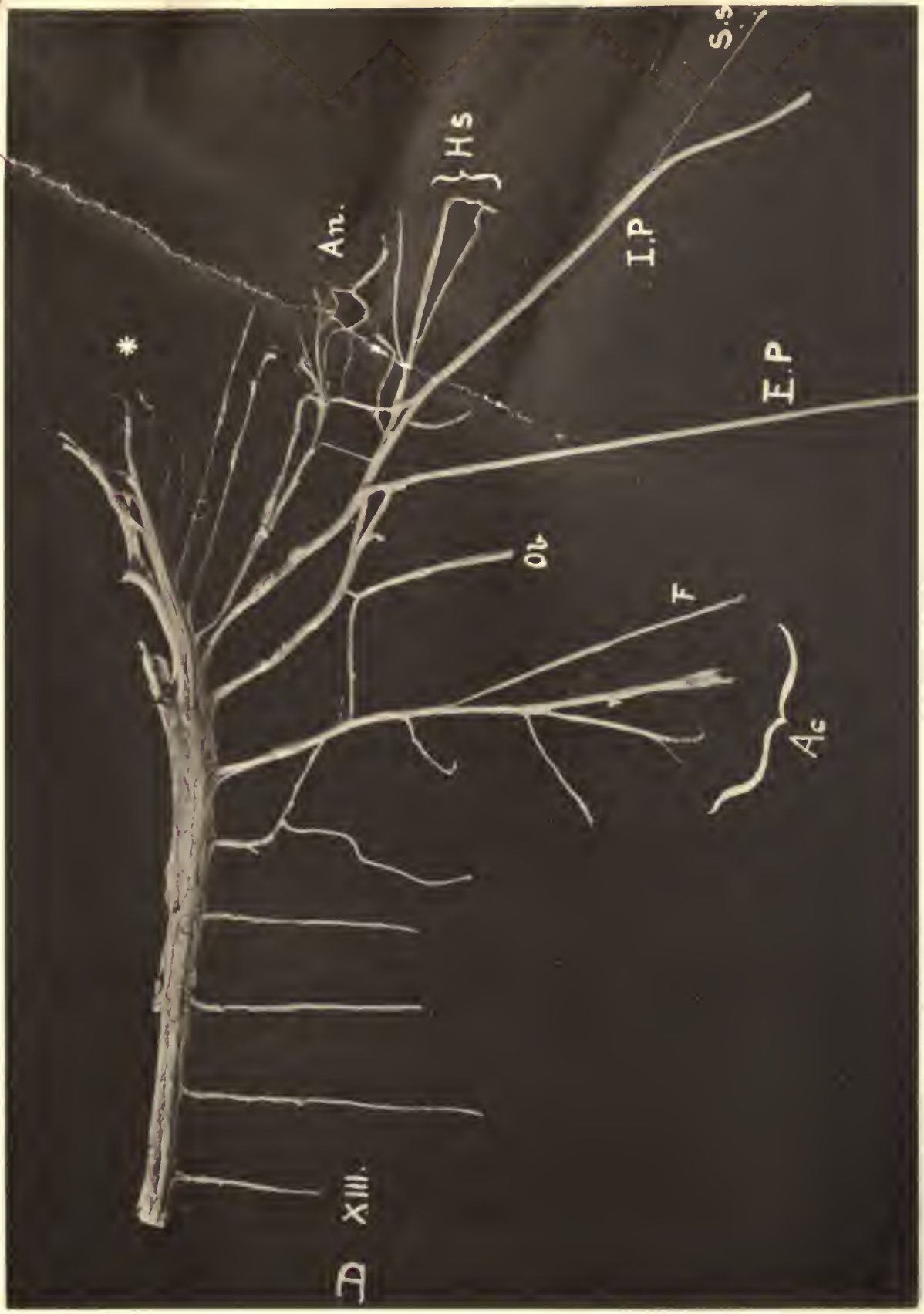
MACACUS RHESUS ADULT ♀



LUMBAR PLEXUS CAT ADULT ♀

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